

THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY

A THESIS SUBMITTED TO THE FACULTY OF THE UNIVERSITY OF
MICHIGAN FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

By EDGAR NELSON TRANSEAU

Ferry Fellow in Botany

PRINTED AT THE UNIVERSITY OF CHICAGO PRESS

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THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY.

EDGAR NELSON TRANSEAU.

(WITH SIXTEEN FIGURES)

I. The Huron River valley.

PHYSIOGRAPHIC FEATURES.

THE Huron River valley, to the botanical survey of which the present paper forms the sixth contribution, is located in the southeastern part of Michigan. As indicated in *fig. 1*, the valley embraces parts of five counties.

Throughout, its surface forms are of glacial origin and, with the exception of the immediate borders of the river, have undergone but slight modification since glacial times. Perhaps its most striking topographic features are the rough morainic hills of its upper and middle courses, and the gently undulating plain of its lower course.

The river has its source in west-central Oakland County in Big Lake, 9 miles (14.5^{km}) southeast of Holly and approximately 40 miles (64^{km}) northwest of Detroit. Starting with an elevation of 950 feet (290^{m}), after a course, extending for 50 miles (80^{km}) generally southwestward and then for another 50 miles (80^{km}) southeastward, it empties into Lake Erie at an altitude of 573 feet (175^{m}) above tide. As is common in areas of glacial deposition, the topography of the drainage basin of the Huron has little of the appearance usually suggested by the term "valley." The upper two-thirds of its course is a winding depression among morainic knobs, lake basins, abandoned glacial drainage channels, and sand plains. Here the river is characterized by long reaches and occasional slight riffles. At intervals it broadens into stretches of lake-like character, as is illustrated by such bodies of water as Commerce, Taylor, Strawberry, Whitewood, and Bass Lakes, each with an area of one-fourth to one-half a square mile ($65\text{--}130$ hectares). The river margin is usually low and swampy.

Its tributaries enter it at every angle, and bring to it the drainage of hundreds of lakes and swamps. Most of these lakes are small,

occupying areas of an acre (half a hectare) or more, but there are several of considerable size. Portage and Whitmore¹ Lakes occupy one and one-fourth to one and one-half square miles (325-390 hectares), while Union, Straits, Four-Mile, Ore, Independence, etc.

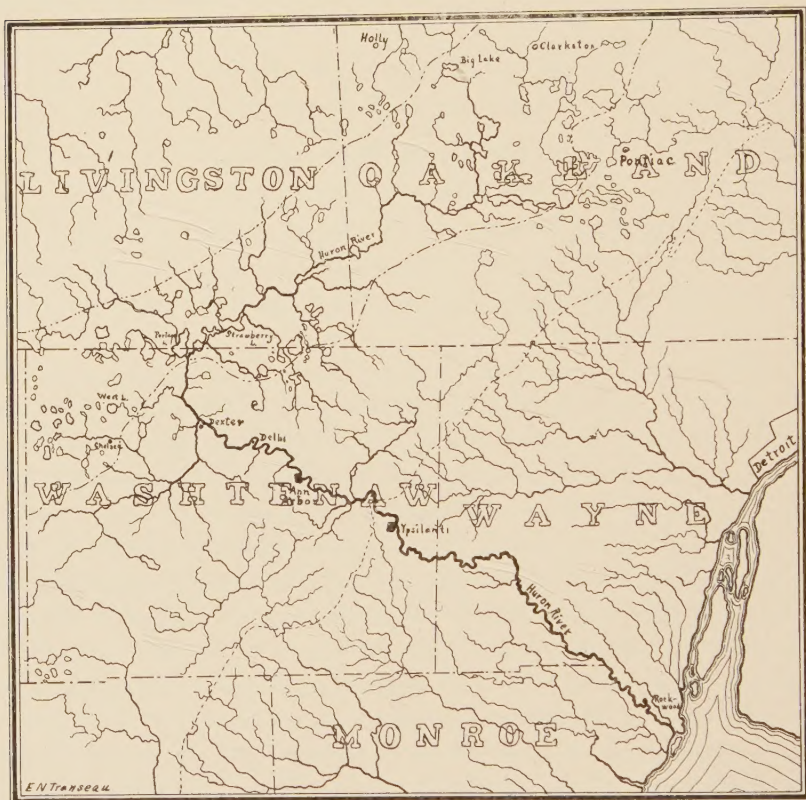


FIG. 1.—Map of the Huron drainage basin. The boundaries of the interlobate moraine are shown by the lines — · — ·. The boundary between the clay morainic belt and the lake plain is marked by the line - - - - -.

cover a fourth to half a square mile (65-130 hectares). A very large percentage of the tributaries lie in flat-bottomed depressions whose surface approximates the ground-water level, consequently producing thousands of acres of swamp and marsh land. Everywhere occur small undrained depressions, some well above the average ground-water level, others containing lakes and bogs. It is also worthy of

¹ Not connected with the Huron River by surface drainage.

note that a large part of the surface drained by the Huron and its tributaries, before it makes the great bend to the southeast below Portage lake, is made up of sand and gravel, composing and accompanying the Saginaw-Erie interlobate moraine. It is a region of steep hills, with occasional dry plains, everywhere penetrated by lakes and swamps.

The country which the river next crosses, beyond the great bend, for a distance of 20 miles (32^{km}) is composed of glacial till plains and clay moraines—a belt extending NE-SW, approximately parallel to the interlobate moraine. Here, although the hills are well marked, the slopes are more gradual and the basins broader. The river is bordered by banks several feet in height, and seldom attains a width of 150 feet (50^{m}).

The last 30 miles (50^{km}) of the Huron River traverses a meandering course sunken from 50 feet (15^{m}) at Ypsilanti to 25 feet (7.5^{m}) at Rockwood below the surface of a glacial lake plain sloping gently southeastward from the morainic belt just described, to the western shore of Lake Erie. The soil is here composed of sand, sandy loam, and—in the vicinity of the lake—clay; the only topographic features aside from the sunken water courses being the several beach ridges and dunes marking the successive stages in the lowering of the glacial lakes, forerunners of the present Lake Erie.

There are, then, three natural divisions of the Huron drainage basin: (1) the loose-textured rough interlobate moraine; (2) the clay morainic belt lying to the southeast of it; (3) and the low-lying plain extending to Lake Erie. Each implies important differences in the way of bog formation and provides edaphic factors which determine to a large extent the nature of the dominant forest covering.

PHYSIOGRAPHIC HISTORY.

The history of these topographic features is for the most part bound up with the retreat of the ice at the close of the last (Wisconsin) glacial epoch. A topographic map of the region lying between Lakes Michigan and Erie shows that the morainic hills so characteristic of the Huron basin are part of a belt of similar physiography extending from northern Indiana well up into the "thumb" of lower Michigan (*fig. 2*). This belt of glacial deposits is directly connected with the

development of reentrant angles along its crest, as the great continental ice sheet² became more and more differentiated into lobes during its retreat (52, 13). In northern Indiana it marks the first areas uncovered, as the mass of ice, pushed forward from the basin of Lake Michigan, separated from that originating in the Lake Huron and Lake Erie basins.

When the Huron River basin was reached, the Saginaw lobe had been developed and lay over the northwestern part, while the Huron-Erie lobe covered all of the territory southeast of the interlobate

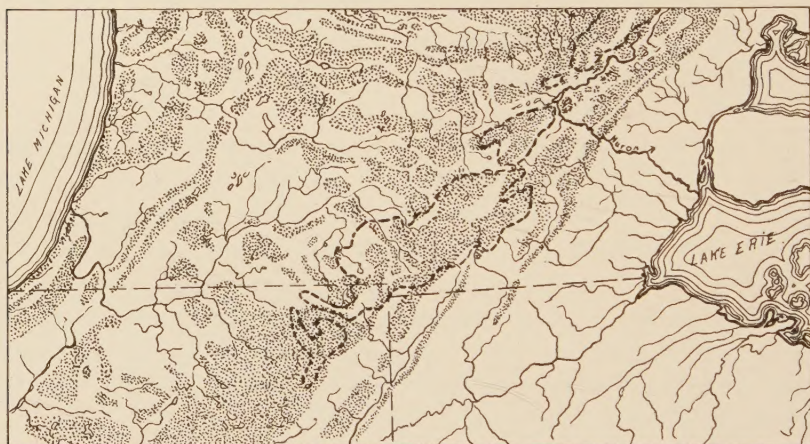


FIG. 2.—Map of southern Michigan, northern Indiana, and northern Ohio, showing "moraines with strong expression." After LEVERETT, U. S. Geol. Surv. Mon. 41, plate 2. The irregular dotted lines mark the 1000-foot (300m) contour.

moraine. The first portion of our area to be uncovered is the triangular gravel outwash apron extending southwestward from Sugarloaf Knob. This was the beginning of the Huron River. Kavanaugh Lake then lay just under the edge of the Erie ice, and Crooked Lake occupied a similar position on the southern border of the Saginaw lobe. As has been recently determined by Mr. FRANK LEVERETT, of the U. S. Geological Survey, the subsequent history of the Huron drainage is most remarkable.

The waters from the glacial drainage at first flowed generally westward, reaching the Kalamazoo River near Albion, thence to the St. Joseph at Three Rivers. At South Bend, Indiana, it crossed

² For general map see no. 55, p. 411. (Bibliography at close of this paper.)

to the Kankakee River, and reached the Mississippi by way of the Illinois.

As the reentrant extended itself further to the northeast, another channel was opened for the Huron drainage westward past Pinckney into the Grand River, and from there to Battle Creek and the Kalamazoo River. Below the city of Kalamazoo it cut across to the Paw Paw River, and reached the Mississippi by way of Lake Chicago.

When the ice of the Erie lobe had retreated as far eastward as Ann Arbor, and all of the interlobate moraine had been uncovered, a third outlet for the waters of the Huron was opened by way of Clinton and the Raisin River, which at that time emptied into glacial Lake Maumee at Adrian (32, *pl.* 20). This lake was drained by the Wabash River into the Mississippi.

As soon as the ice margin passed the clay morainic belt already described, the Huron reached Lake Maumee at Ypsilanti by way of its present channel. But Lake Maumee had meanwhile changed its outlet to the northward, its drainage going by way of Imlay (53) to the Grand River, Lake Chicago, and the Mississippi (32, *pls.* 21, 23, 26).

Later the Erie basin was entirely freed of ice, and its water for the first time flowed eastward into the Ontario basin (glacial Lake Iroquois), and thence by way of the Mohawk to the Hudson. With the clearing of the St. Lawrence channel the present system was inaugurated.

Aside from the physiographic interest connected with their early history, these glacial drainage channels are of distinct biological interest. They furnish continuous lowland habitats extending in all directions. In so far as they are represented by broad, open valleys, and connect with tributaries of the northern Ohio valley, they provide important highways for the dispersal of southern river-valley species.

FORESTS.

The three topographic divisions already described exhibit marked differences in their forest aspect. On the lake plain we find the richest and most mesophytic of the forest types. This lowland habitat is a continuation of the northern Wabash valley, and it is not surprising that its flora should be of much the same character. Here

we find the greatest variety of tree species, among which are *Fagus atropurpureus*, *Quercus rubra*, *Ulmus americana*, *Platanus occidentalis*, *Acer saccharum*, *Tilia americana*, *Acer saccharinum*, *Fraxinus americana*, *Gleditsia triacanthos*, *Liriodendron tulipifera*, *Gymnocladus dioica*, *Cercis canadensis*, *Asimina triloba*, and *Celtis occidentalis*.

The clay morainic area is dominated by *Quercus rubra*, *Q. alba*, *Q. velutina*, *Hicoria ovata*, *H. glabra*, *Acer rubrum*, *Ulmus americana*, and *Quercus macrocarpa*.

In the region of the interlobate moraine the disappearance of the more mesophytic forms is quite marked. The forest is there largely composed of *Quercus coccinea*, *Q. macrocarpa*, *Q. velutina*, *Q. alba*; and as we go northeastward these become associated with *Pinus strobus*. *Quercus prinoides* forms a characteristic shrubby growth along the roadsides and in waste places.

Such is the forest background in which are set the thousands of acres of bog and swamp, and to which the groves of *Larix laricina* exhibit a marked contrast. These tamarack areas are to be seen on all sides in the region of the interlobate moraine; they are quite common in the clay morainic belt, but are practically wanting on the lake plain.

As one follows along the morainic country from northern Indiana into the "thumb" of Michigan, he passes from a region dominated by a rich mesophytic broad-leaved forest to one of conifer and xerophytic broad-leaved ascendancy; from a region whose low grounds are characterized by a swamp flora to one in whose depressions the bog flora reaches a high state of development. In this connection it is interesting to note that one finds this gradual change epitomized in the Huron valley as he goes from its mouth to its source.

METEOROLOGICAL CONDITIONS.

Under this head we shall consider the general meteorological conditions of the Huron basin, and compare them with the meteorological conditions found about the center of the distribution of bog plants (55, p. 406). In general, this center extends from Lake Winnipeg through the upper Great Lake region down the valley of the St. Lawrence to the Atlantic coast. It is in the coast provinces, however, that the bogs reach their highest development, in the form

of the “raised bog.” Certain temperature phenomena associated with the bog habitat will be discussed in connection with the analysis of the life conditions obtaining in bogs.

Rainfall.—In the following table is given the mean monthly and annual precipitation for seven stations located within or near the Huron basin. As their individual variation is but small, it is probable that the average for the stations gives a fair estimate of the rainfall and its distribution. Appended are the corresponding records for the maritime region of eastern Canada:

MEAN PRECIPITATION IN INCHES.

Station	Alt. feet a.t.	Rec- ord for Yrs.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann.
Ann Arbor.	930	23	1.09	2.19	2.12	2.88	3.72	3.39	2.82	2.45	2.58	2.82	2.77	2.35	32.08
Ypsilanti..	736	18	1.07	2.61	2.48	2.24	3.98	4.02	3.09	2.24	2.63	2.70	3.29	2.32	33.60
Jackson...	927	6	2.06	2.21	3.14	1.26	3.22	3.02	2.47	1.76	1.74	3.61	2.87	1.56	28.02
Annper...	924	11	1.08	2.19	2.42	2.60	3.38	2.44	2.66	2.85	1.93	2.04	2.64	1.77	26.05
Ball Mt....	932	13	1.73	1.76	2.07	2.12	3.52	3.13	2.47	2.59	2.62	2.66	2.71	2.39	29.72
Birm'gham	860	15	1.91	2.00	2.32	2.53	3.36	3.15	2.56	2.38	2.33	2.51	3.02	1.88	29.95
Average.			1.94	2.16	2.42	2.27	3.53	3.19	2.68	2.38	2.30	2.73	2.88	2.03	30.22
St. John, N. B. (18)		?	5.55	3.93	3.80	2.50	3.66	2.72	3.29	4.64	3.08	4.13	4.71	5.16	47.17
Halifax, N. S. (51)		22	5.63	4.94	5.15	4.00	4.43	3.68	3.43	3.96	3.53	5.21	5.26	5.52	57.74

It will be noticed from the above data that the precipitation is quite evenly distributed throughout the year. It reaches its maximum during the months of May and June, when the vegetative processes of the bog plants are most active. It approaches its summer minimum during July and August, when the temperature commonly attains its greatest height. The former implies that the water level in the bogs is kept at or above the surface of the substratum for weeks at a time. The latter involves strong transpiration on the part of the vegetation, when the water supply must be drawn for the most part from the substratum. The average number of rainy days during the past five years is one hundred per annum.

The average snowfall in this region during the five years, 1898 to 1902, amounts to 38.4 inches (975^{mm}). In the case of the bogs this thickness is usually increased by the drifting of snow from the surrounding hills. Observations during the past two winters show that the bogs are covered by ice to a thickness of a foot (30^{cm}) or more.

Consequently, low shrubs, and herbs which pass the winter by means of underground stems, are well protected from low temperatures and sudden temperature changes. The ice further results in lowering the temperature in spring and in retarding the beginning of favorable growth conditions.

The percentage of sunshine is not published by the several stations, but the number of clear and partly cloudy days is stated. The numbers from the various stations show marked differences, due to different standards established by the observers; but perhaps these are largely eliminated in the average. If we take the average number of clear days, add to it one-half the number of partly cloudy days, and divide by the number of days in a year, we obtain a percentage of forty-six. This probably approximates the percentage of sunshine.

In comparison with the rainfall data for Halifax and St. John, it is notable that in the latter localities the mean rainfall, both monthly and annual, is considerably larger. The annual precipitation exceeds that of the Huron valley by fully 20 inches (50^{cm}), or about 40 per cent. Finally, the sunshine percentage is slightly lower, being 39 for Halifax and 42 for St. John.

Temperature.—The following table exhibits the monthly and annual means for the several stations already cited:

MEAN TEMPERATURE IN °F.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann.
Ann Arbor.....	22.2	23.1	30.6	45.4	53.2	67.3	72.0	69.3	62.5	49.9	36.4	27.1	46.6
Ypsilanti.....	25.9	24.2	32.3	46.7	58.1	63.5	71.1	69.7	61.8	49.9	36.7	27.6	47.3
Jackson.....	26.1	20.3	32.7	47.5	59.4	69.4	74.8	71.8	64.8	54.7	37.7	26.5	48.8
Annperé.....	24.7	21.7	31.3	50.2	56.5	68.4	71.8	67.6	63.0	49.8	35.9	26.7	47.4
Ball Mt.....	22.6	21.4	27.6	45.3	56.0	66.9	70.0	68.1	62.2	49.5	35.9	27.1	46.0
Birmingham.....	23.1	22.8	30.4	46.5	57.3	69.1	72.2	68.4	61.5	49.7	36.7	27.0	47.1
Average.....	24.1	22.2	30.8	46.9	56.7	67.1	71.9	69.1	62.6	50.6	36.5	27.0	47.2
St. John, N. B.....	18.6	18.7	26.3	38.6	48.8	56.3	61.0	61.3	55.6	44.7	36.1	23.7	40.8
Halifax, N. S.....	22.0	22.7	28.7	38.2	48.7	57.6	64.2	64.8	58.2	48.0	38.2	27.0	43.2

The table shows that the temperature conditions are comparatively uniform throughout the basin. The maximum average temperatures occur in July and August. But the significance of the data becomes more apparent, in so far as the bog vegetation is concerned, when they are compared with those of St. John and Halifax (*fig. 3*). It is to be noted that, although the average temperature for June,

July, and August of the Huron basin is 8.6° F. (4.8° C.) higher, its rainfall during the same period is less by 2.6 inches (66 mm). There can be little doubt as to the effect of such differences upon the growth of the bog species, especially the sphagnum whose moisture supply is more directly dependent upon atmospheric water than upon the

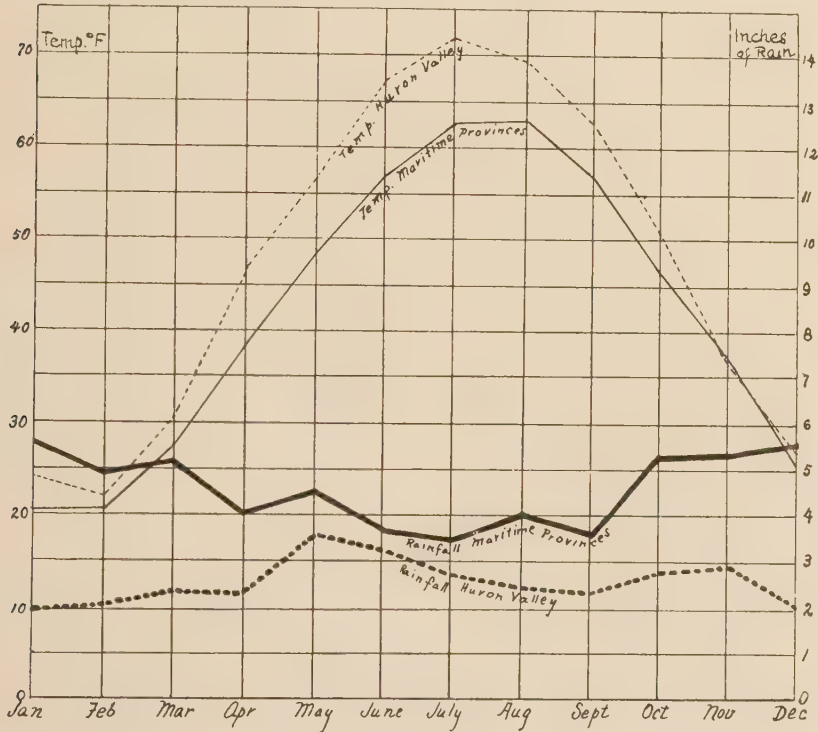


FIG. 3.—Curves of rainfall and temperature conditions in the Huron basin compared with those of the maritime region of Canada.

soil solution. Again, the occurrence of high temperature with decreased precipitation means the production of conditions impossible for the development of the “raised bog,” if not unfavorable to the highest development of the “flat bog.”

Since bogs attain their maximum development in a region of great rainfall and comparatively low temperatures, it is reasonable to infer that the extremes of summer heat become peculiarly significant in this region. Examination of the weather records shows that

temperatures of 97–100° F. (36–38° C.) are likely to occur every year, and that temperatures approximating these may be prevalent for several days in succession each season. When these extremes coincide with periods of drought, they must act as important checks on the growth of the bog plants, especially the sphagnum. As we pass from northern Indiana along the moraine into Michigan, the gradual increase of bog development, of the variety of bog species, and of the areas covered by sphagnum is very marked. Although other factors are involved, this increase may be correlated with a decrease in summer temperature extremes.

II. The bogs: their development and ecological conditions.

PHYSIOGRAPHIC ORIGIN OF THE LAKE AND BOG BASINS.

In connection with the special consideration of the bog flora, it is of interest to note the origin of the depressions in which this flora has developed and flourished. Indeed, in the morainic belt of the Huron basin it would seem that among the agencies which have produced important topographic changes since glacial times, the bog plants stand near the head of the list. Stream erosion and deposition have been slight, while lake basins have been filled and the level of depressions generally raised by the deposition of plant débris.

As no attempt has as yet been made at the mapping of peat deposits and muck soils, no reliable estimate of the total amount of aggradation accomplished by plant agencies can be made. Yet the frequency with which in field work one encounters peat soils, in various stages of making or decay, suggests that in the aggregate such deposition has been most effective in this region. The northwest quarter of the Ann Arbor topographic map, which embraces an area of about 215 square miles (55,700 hectares), located in the morainic portion of this basin, indicates approximately 43 square miles (11,500 hectares)—20 per cent.—as swamp land. It is probable that at an early time this area was very much larger, but with the settlement of the land many extensive areas have been drained and only the dark humous soil remains to suggest its past history.

The most frequent source of lake and bog basins is here found in connection with the deposits made by glacial drainage. Among the vicissitudes attending the retreat of a glacier are the occasional

detachment of blocks and masses of ice through differential melting (19). If these detached masses happened to be in the line of the overloaded glacial drainage, they became covered to a greater or less extent by sand and gravel. Owing to the poor conduction of heat by such deposits, they melted with extreme slowness. Where this latter process was prolonged until the drainage line had been abandoned or the stream had ceased depositing, subsequent melting brought about a settling of the deposits and the production of basins. Sister, Kavanaugh, and Crooked Lakes are examples of this type.

In the case of the chain of lakes which form a part of the Huron River in northwestern Washtenaw County, and such lakes as Portage, Tamarack, Ore, and Bass, according to LEVERETT, there was an additional settling of the fluvio-glacial deposit itself. This latter process has been of the greatest importance in the development of extensive bog areas. In the Portage Lake region this settling has amounted to as much as 40 feet (12^m) in certain places, and has resulted in reducing many hundreds of acres of land to the ground water level.

Throughout the belt of till plains occur shallow marshes, sometimes drained, but usually by a sluggish meandering stream, itself impeded by the growth of swamp plants. These basins are the natural expression of the unequal deposition of glacial material. Till plains result from a comparatively rapid retreat of the ice; hence the depressions are usually shallow, and have been mostly filled with peat to the level of the present drainage. The several small lakes lying to the west of Dexter are examples of basins not yet obliterated.

Where the retreat of the glacier is slow and deposits are made to a great thickness about the edge of the ice, kame or "knob and kettle" topography results. The basins of such areas are characterized usually by high margins and comparatively steep slopes. West, Silver, North, Island, and South Lakes may be cited as examples.

As we know from remains discovered in peat deposits, among the animals inhabiting this region in early postglacial times were the mammoth, mastodon, bison, peccary (*Platygonus compressus* LeConte) (57), elk, and "big beaver" (*Castoroides ohioensis* Foster). The last named is not a beaver (34, p. 256), but is more nearly related to the Coypu rat of South America. The common beaver

(*Castor canadensis* Kuhl) has been an important factor in the creation of bog areas (37), and in the extension of areas already existing, by the building of dams. The beaver was found in this section when it was first settled, but the last known specimen was killed sixty-nine years ago. The occurrence of peat deposits several feet in thickness and covering quite large areas, bordering streams, whose channels lie deeply sunken in the deposits, seems to find its best explanation in this manner. But little field work has been done on the relation of beavers to the peat deposits, and examples are still too hypothetical to cite in this connection.

BOG AND LAKE VEGETATION.

Of the plants which might come into a new land area containing basins, such as was laid bare on the retreat of the glaciers, none is better adapted to rapid migration than the group of aquatic plants. Whether we have in mind the smaller submerged varieties or the partially submerged littoral species, their wide geographic distribution and uniform associations bespeak their evident solution of the problems of dispersal. The fact that deposits of peat and marl have been found in northern Indiana and lower Michigan to a thickness of 40 feet (12^m) would indicate that in these particular basins the vegetation must have obtained an early foothold.

Concerning the deposition of marl, it is of interest to us only in so far as it becomes an agent of aggradation in the basins. In the reports (5, 42, 21) on the marl deposits of Indiana and Michigan, many examples are cited where the marl forms the underlying substratum of peat deposits. That its deposition to a large extent is due to plant life has been shown by DAVIS (9, 10). The plants most concerned with this process are the Characeae and Cyanophyceae (Schizothrix, Zonotrichia). They are probably aided by certain mollusks, and perhaps also by chemical precipitation. As for the Characeae and Cyanophyceae, they have a wide range of habitat in different lakes, and may occur in deep or shallow water and on various rock substrata. Where they come into competition with shore species, the rank growth of the latter usually precludes their existence in sufficient amount to be of importance in marl formation. Where wave action is strong, the chara is confined to deeper water,

but the blue-green algae may be present up to the water's edge, in such situations frequently forming marl pebbles. The lower limit of existence is largely determined by the transparency of the water, and may lie between 20 and 30 feet (6-9^m). Of the littoral plant associations there are commonly two quite distinct divisions, the outer made up largely of submerged or floating pondweeds and water-lilies, the inner of half-submerged rushes and sedges. Both are concerned in the process of peat formation. Under such conditions there naturally develop, in regions of calcareous underground waters, an outer zone of chara dominance and marl deposition, and an inner zone of pondweed-sedge dominance and peat deposition. Variations in the slope of the bottom, in the amount of wave action, in the presence of shore currents, and in the color of the water, determine whether one or both of these processes shall go on, and to what extent these activities are kept distinct or grade into one another.

In the case of the peat, however, the process is not dependent upon water species alone. They act merely as forerunners of a denser and more luxuriant vegetation which frequently is of greater quantitative importance. Briefly, we may note here that in the case of the bogs, unlike that of the swamps, the plants which develop on the margin, especially *Carex filiformis* and forms of *Eriophorum*, are able to secure all of their food materials from the water and air and build their own substratum. This tangle of roots and rhizomes usually attains a thickness of several inches, and on account of its low specific gravity floats on the surface of the water. Upon this foundation the sphagnum and bog shrubs advance, adding their quota to the débris. Later, these are followed by such tree forms as the tamarack. Coincident with this increased weight and augmented rate of deposition, comes the progressive submergence of the floating substratum, and its gradual disintegration and humification. The accompanying *fig. 4* will serve to illustrate this process.

Within the last two years much has been promised toward the utilization of the peat deposits in this region for fuel purposes. Companies have been organized, and the machinery necessary for the drying and consolidating of the peat has been much improved. At Capac and Chelsea, factories have been erected, and attempts are being made to place the industry on an economic basis. If these

ventures prove successful, we may hope for an interesting body of scientific information to come from the study of bog sections. The work of ANDERSON, LAGERHEIM, SERNANDER, WEBER, and others in Sweden and Germany, gives indication of the data concerning postglacial migrations of plants and animals, and climatic changes, which will be obtainable when our bog deposits become of economic importance.

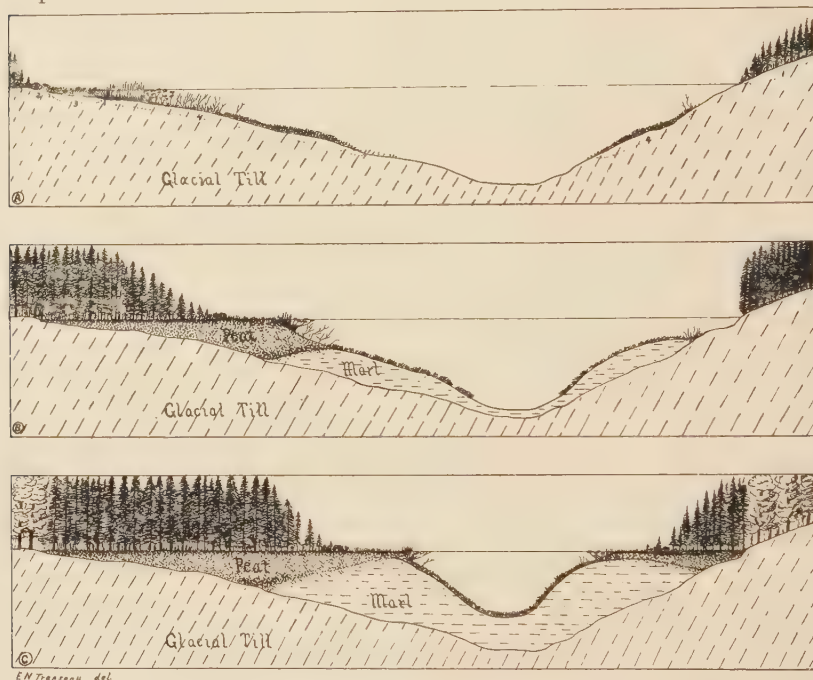


FIG. 4.—Diagrams illustrating three stages in the development of peat and mar deposits in lake basins. In drawing the figures it has been assumed that the rates of marl and peat deposition are approximately equal. * The peat accumulates most rapidly on the western side of the basin. On the east side a common effect of wave action is illustrated. The process of peat formation is hindered, while that of marl deposition goes on until the aggradation of the bottom reduces the force of the waves sufficiently to allow the bog plants a foothold. A represents conditions in early postglacial times when these basins acquired their first flora. The several plant societies represented are (1) conifer (2) bog shrub, (3) bog sedge, (4) aquatic, the outermost division of which is the chara association. In B the conditions for the growth of plants belonging to the northeastern conifer forest formation have reached their optimum. C represents present conditions in southern Michigan. The plants belonging to the southeastern broad-leaved forest formation, being climatically favored, occupy the areas of mineral soils, while the conifers are almost restricted to bog areas.

THE GEOGRAPHIC DISTRIBUTION OF PEAT DEPOSITS.

In North America the distribution of recent peat deposits may be conveniently summarized under two heads, genetically unrelated: (1) those of glaciated regions; (2) those of the coastal plain.

The peat of the glaciated area constitutes the great bulk of these American deposits. The southern boundary of this region is marked by a line passing westward from central New Jersey through northern Pennsylvania and Ohio, central Indiana and Illinois, thence northward through southern Wisconsin, northwestward to the Minnesota valley and the Red River of the North in Manitoba, westward through northern Assiniboia and southern Alberta to the Rockies. Here the boundary is deflected southward into Montana, but in crossing toward the coast it is again carried northward into British Columbia, and finally southward among the Cascades of Washington to the Pacific Ocean.

Along this southern border the peat deposits are exceedingly scattered and make up a small fraction of the total land surface. They have accumulated under water in depressions among the recessional moraines. As we go northward, the relative proportion of peat bogs and peat deposits regularly increases, and there is a notable tendency toward the accumulation of pure humus in situations other than depressions containing water. When the tundra or "barren ground" is reached, the accumulation of humus is almost universal. The contrast with our own region is well brought out in RUSSELL'S account of the tundra (43, p. 129). The vegetation

grows rapidly during the long, hot, summer days, dies below and partially decays, but becomes frozen and has its complete destruction arrested, while the dense mat of roots and stems continues to thrive. In this way an accumulation of partially decayed vegetable matter is formed, which increases in thickness from year to year by additions to its surface. The process is similar to that by which peat bogs are formed in temperate latitudes, except that the partially decomposed vegetation becomes solidly frozen. It is in reality an example of cold storage on a grand scale.

Under existing climatic conditions there does not seem to be any limit to the depth such deposits may attain. The amount of carbonaceous material already accumulated in the tundras of America and Asia must equal that of the most extensive coal field known.

South of the boundary above described, peat deposits of consider-

able extent are occasionally met with. In the region of the great plains they are sometimes found beneath a surface covering of sand and wind-blown deposits. TODD (54, p. 121) has mentioned the occurrence of such peat deposits in eastern South Dakota. BARBOUR also reports such deposits from central and eastern Nebraska (2). On the basis of their field relations and certain fossils which they contain, they are believed to be of Glacial and early Pleistocene age. If the plant materials of these deposits could be carefully worked over with reference to their successive floras, we might hope for some new light on glacial climate, since a part of the deposits are beyond the margin of the Wisconsin ice sheet. But even their location and existence give evidence of climatic change, and plant and animal migration. Although now widely separated from the region of active bog formation, they are historically connected with this division.

Among the mountains of both the eastern and western United States, bogs and swamps are to be found in association with mountain lakes. More frequently than otherwise these depressions are connected with former local glaciation, perhaps the most frequent situations being those afforded by the damming back of water by terminal and lateral moraines. Basins for peat accumulation are also found in solid rock made by glacial erosion. The conditions here are quite similar to those of the north, the altitude bringing about the same general effect as the latitude. The analogy is still further shown on mountains in moist regions where alpine meadows are strongly developed. Not only are the plants related to those of the tundra, but the deposition of peat or humus is again irrespective of basins.

In many places east of the great plains there is another type of situation not directly connected with glaciation, but in which vegetable débris may accumulate to considerable thickness, viz., about the débouchure of cold springs. Toward the north these springs may bring about humus accumulation on slopes, but further south peat is usually associated with pools and small lakes.

The second group of situations in which peat accumulation takes place on a grand scale, are those associated with coastal plain phenomena, such as the rising and sinking of the land, the irregular deposition of alluvial materials in deltas, and the extension of the

land through reef building. These swamps have been described by SHALER, KEARNEY, JULIEN, and others (46, 26, 24, 7). They reach their greatest development in eastern Virginia, North Carolina, Florida, and the Mississippi floodplain. They may contain either salt or fresh water, and their vegetation is noted for its density and luxuriance.

The geographical distribution of peat deposits is of interest in this connection because it points to certain factors which contribute to the preservation of humus materials. Certainly in arctic latitudes the most significant factor is the low temperature, for humus accumulates to great thickness even with a scant vegetation. In the northern states and southern provinces of Canada, peat is associated with basins containing stagnant water or cold springs. The annual increment from the vegetation is greatly increased over that of the tundra. Mild temperatures and stagnant waters combine to preserve the plant débris. When we come to the coastal plain swamps of the southern states, this process takes place only where a luxuriant vegetation is combined with areas of stagnant water of considerable depth.

To put it sharply, we may say that, in spite of the scant vegetation, the cold of the tundra results in peat accumulation. In temperate latitudes, mild temperatures and stagnant water combine to prevent the complete disintegration of a vigorous vegetation. In the south, in spite of the high temperature, the luxuriance of the vegetation and stagnant water unite to make peat formation possible.

THE PROCESSES INVOLVED IN PEAT FORMATION.

When for any reason the living protoplasm in a plant or any of its organs is brought to the condition of death rigor, the continuance of this state for a prolonged period inaugurates certain chemical and physical processes which result in the breaking down of the exceedingly complex structures and compounds making up the living plasma. Among the first outward signs of such disorganization is the loss of water. The cells of soft tissues lose their normal form, and in any case the tissue becomes more or less filled with gases. The protoplasts as such disappear, and in their place granular carbohydrate and proteid bodies are to be found.

Aside from the mineral substances composing the ash of such bodies, the organic compounds are made up for the most part of carbon, hydrogen, and oxygen. In the case of the proteids, there are added to these nitrogen, sulfur, and phosphorus. As to the exact nature of the compounds existing in the dead material, aside from the carbohydrates, very little is known. The same statement holds as to the nature of the decomposition which goes on without the intervention of saprophytic organisms. But it seems probable that oxidation does occur. This action, then, is the beginning of the more comprehensive process known as peat formation.

When plants or their organs die, under ordinary circumstances they are at once attacked by fungi and bacteria. The progress of dissolution is then greatly hastened, and the final disintegration is more complete. According to the operation of certain external factors, the destruction may involve two very different groups of organisms and result in bodies of very different chemical and physical properties. These two processes are known as *eremacausis* and *putrefaction* (61, 39).

Where access to oxygen is accompanied by favorable temperature and moisture conditions, the first of these processes, *eremacausis*, takes place. The formation of ordinary soil humus may be cited as an example. That oxygen plays the important rôle has been demonstrated both by experiment, and by the analysis of the gaseous and solid products. It has been shown, for example, that soils in which *eremacausis* is in progress contain CO_2 and O in inverse proportion to one another. Under constant volume, as the one increases the other decreases. It has been also shown by experiment that the process is wholly dependent upon the activities of certain lower plants. Among these members of the genera *Mucor*, *Aspergillus*, *Penicillium*, *Saccharomyces*, *Micrococcus*, *Bacterium*, *Spirillum*, *Crenothrix*, and *Beggiatoa* are most important.

The carbohydrates are by this means broken down to CO_2 and H_2O . The albuminoids and amides constitute the principal forms of the nitrogenous materials. Under the influence of these organisms, especially their katabolic processes, the oxygen unites with the carbon to form CO_2 , the S is oxidized to H_2SO_4 , the P to H_3PO_4 , and the H to H_2O . The first form in which the nitrogen reappears is that

of ammonia. This is at once attacked by the nitrifying bacteria, and changed successively to the form of a nitrite and a nitrate. The two latter changes again involve the addition of oxygen.

If we consider only the temperatures occurring in nature, we may say that these activities increase regularly with the temperature. As to water conditions, it has been shown that in air-dry soil *eremacausis* is practically wanting, and that when the soil is filled with water it is reduced to a minimum. Between these two extremes lies an optimum at which there is sufficient moisture for the life of the organisms, and yet not enough to interfere with the diffusion of oxygen. An acid condition impedes, and a slight alkalinity favors, the production of both the carbon and the nitrogen compounds.

Eremacausis is then essentially a process of oxidation, brought about by lower organisms, whose activities are favored by a high temperature, a slightly alkaline medium, and free access to the air. Its products are simple compounds which may furnish food materials for the higher plants living on the substratum in which they are formed.

By putrefaction is meant that process of disintegration which occurs when organic matter decays in the absence of oxygen. Here again organisms are involved, but they belong for the most part to the anaerobes, and are wholly forms of bacteria. The process is essentially one of reduction.

Carbon dioxid is again the principal gaseous product, but its relative amount is greatly reduced. Along with it CH_4 , H_2 , H_2S , H_3P , N_2O , and N are produced in small quantities. In the manufacture of the carbon dioxid the oxygen is not only derived from the organic matter, but also from nitrous oxid, nitrites and nitrates which may be present. In the decomposition of cellulose, carbon dioxid and methane result from the hydrolysis of the cellulose molecule. Albumins at first break up into amido-acids, nitrogenous compounds of the aromatic series, and other little-known bodies. If the decomposition continues, the amido-acids in turn form ammonia and compounds of the fatty-acid series. The latter substances may still further disintegrate to carbon dioxid, hydrogen, and methane. Depending upon the stage in the progress of decomposition, we may find complex organic compounds, organic acids, and their salts, or comparatively simple substances.

As to the influence of external factors, high temperatures increase the rate of disintegration, while the presence of acids prevents its continuance, due to the killing of the bacteria involved. It is to be noted that the products of putrefaction, both intermediate and final, can be of little use in furnishing food materials for the higher plants.

With these two processes in mind, we may now consider the matter of peat formation as it occurs in this region. We have already seen how the substratum is being extended at the edge and renewed at the surface by the plants forming the outer zone of the bog vegetation. It consists of sedges, especially forms of *Carex* and *Eriophorum*. Each year these plants send up stems and leaves from the matted rhizomes. At the approach of winter these are killed, and the snow later on aids in bringing them down to the water level. In the spring the water covers almost the whole of this zone to the depth of several inches. With the gradual lowering of the water level and the coming of warmer temperatures, the conditions for *eremacausis* are made favorable. If the water is approximately neutral in its chemical reaction, the fungi and bacteria begin the work of disintegration, which if continued would result in the complete destruction of the vegetable *débris*. However, on account of the great demand for oxygen, the process can be carried on only near the surface of the water. Even at a depth of a few centimeters the rate of oxygen diffusion is so small, as compared with the demand for it, that practically all aerobic bacterial action is prevented. All of the surface waters which I have examined have been found to be teeming with bacteria.

Close upon the extension of the bog-sedge zone comes the sphagnum-heath zone. Here the surface is characterized by hollows and elevations, the latter frequently due to the upward growth of the sphagnum beneath the shade of the heath plants, but in some cases due to the building of mounds by ants. In the hollows the water stands above the substratum throughout a large part of the year and even during dry periods lies just at the surface. Unlike the sedges, the principal plants of this zone are evergreen. The sphagnum forms a continuous mat of living plants several centimeters in thickness, through which all of the oxygen must diffuse before it can be available for the *eremacausis* of the dead plant-material beneath. The *cassandra*, *cranberry*, and *andromeda* which compose the bulk of the shrubby vegetation add to the *débris* largely

by their leaves and underground stems. The former fall to the substratum as they die, but not at the close of each vegetative period. Consequently they are soon lost among the sphagnum, and there is no distinct annual layer added.

But beneath this layer of possible aerobic activity, the material would seem to be subject to putrefactive agencies. And there can be no doubt that such destructive processes are carried on in those situations in which the acidity of the soil solution does not preclude the existence of the anaerobic bacteria.

Among the taller shrubs and trees, such as *Vaccinium corymbosum*, *Aronia nigra*, and *Larix laricina*, the defoliation takes place each autumn. As these plants are of relatively large size, the bulk of the material forms a noteworthy annual addition to the substratum. When to this is added the twigs and small branches which fall each season, we can understand the fact that the substratum is almost entirely free of surface water. Usually the ground-water level lies 5-10 cm below. But the substratum has a high water-capacity and is kept constantly moist. Where the sphagnum covering is wanting for one reason or another, the dark color of the surface peat shows how much more complete is its disintegration as compared with that of the other zones. This condition is made possible by its position relative to the ground water. On the other hand, as will be shown later, the temperature conditions are more favorable in the zones of herbaceous and shrubby vegetation.

Most of the basins in which peat formation is going on actively, are subject to considerable variation in water level, both seasonal and annual. During the last two years the rainfall has been considerably above the normal in lower Michigan, and many of these bog areas were flooded. At West Lake, for example, a large part of the tamarack area was covered with water to a height of several inches above the level of the roots. Most of the basins are also subject to higher water level in the spring and during prolonged rainy periods. Accompanying such changes there are great differences in the rate and manner of decay. High water, in so far as it excludes oxygen, favors putrefaction; if it comes as a result of heavy rains, it decreases the acidity of the soil solution, increases its oxygen content, and at least for a short time favors the growth of the saprophytes causing eremacausis. Low water level exposes a much greater bulk of the

substratum to disintegration, and favors the carrying away of the products of decomposition; in general, it favors eremacausis. In the samples of water which I have examined at various times from the same depressions, there have been marked variations within short periods of time in the color of the water and in the presence of such animals as *Daphnia* and *Cyclops*. No attempt has been made to count or even separate the bacteria present, but it is probable that they too vary with the color of the water and the animal life.

When the bog land has been cleared and ditched, the marked increase in the rate of decay is apparent. *Eremacausis* becomes exceedingly active, and in the course of a few years the substratum is reduced to a brownish-black, pulp-like mass. If continued, this goes to form "muck," a substance which when dry is powdery and somewhat resembles soot. During these processes of decay there occurs a succession among the organisms present. The accumulation of disintegration products makes the medium unfavorable for the continued existence of the organism involved in their production. At the same time it may furnish optimum conditions for the development of other forms. An acid medium favors the growth of the *Phycomycetes*, while alkalinity favors the bacteria. In such regions as this, where the underground waters are alkaline, the latter fact, together with fluctuations in the ground-water level, may have an important bearing upon the presence of more thoroughly decayed peat and of a distinct depression about the margins of many of the bogs.

If to the factors of relative scarcity of oxygen and the acidity of the soil solution is added the occurrence of temperatures considerably lower than those of the surrounding uplands, it is not difficult to understand why a large part of each year's vegetative products should escape complete destruction. In our estimate of the bog substratum as a habitat for higher plants, the strong competition with the microscopic plants to which the former are subject in the acquisition of oxygen for their underground parts, must be emphasized.

THE PHYSICAL AND CHEMICAL PROPERTIES OF PEAT.

The peat formed through the agency of the bog sedges and their attendant plants has a fibrous and matted appearance. The structures of the various dead stems, roots, and leaves have suffered but slight

alteration. They were originally strongly cuticularized, and this has aided in their preservation. The color is commonly a pale yellowish-brown. During life these plant materials become strongly matted and interwoven, and this structure frequently persists. It is this structure that gives to the *Carex-Eriophorum* zone in many lakes its strength to support heavy bodies. A man's weight will carry the substratum a foot beneath the surface of the water, but it seldom breaks under the strain. In the case of lakes where this zone is unusually developed, it may cover a large part of the lake surface and be of great importance in the filling in of peat. In such cases the deposition takes place largely by the gradual falling of material from the under side of the floating substratum. On account of the slight weight of the material, it does not descend and produce a compact deposit on the bottom, but forms a sort of thick liquid peat.

The sphagnum-shrub zone, where well developed, usually shows a brown peat beneath it. It is composed largely of sphagnum and the semi-decayed twigs, rhizomes, and leaves of the other plants. It is distinctly fibrous, but of a type different from that of the sedge zone; the fibers are short, and the material is not nearly so tenacious.

Under the tamaracks a large part of the annual peat increment is made up of the tamarack needles, though mosses (*Hypnum*, *Sphagnum*, and *Polytrichum*) usually are of importance in this connection. The color is reddish-brown and darker than that of the shrubby zone. The fibrous structure is still less apparent, though present.

When these bogs have been burned over and partially drained, there frequently comes in a dense ground covering of moss (*Polytrichum*). In such cases the peat continues to accumulate, largely through the agency of this plant. In such situations the peat is a reddish-brown, and the plant structures have practically disappeared through decay. Below the upper layer, the peat when moist has the sticky, clayey properties of well-decomposed peat.

One other well-marked stage is shown in the areas of muck land now under cultivation to onions and celery. Under the influence of drainage and tillage, the disintegration is nearly complete. All plant structures have disappeared, the humous acids have been largely neutralized or washed out, and there is left only a fine, powdery, brownish-black "muck."

The following table shows some other physical properties of these several varieties of peat.

	Eriophorum Zone Peat	Fresh Sphagnum	Cassandra-Sphagnum Zone Peat	Tamarack Zone Peat	Chelsea Bog Peat	Onion Marsh Muck
H ₂ O-capacity % by volume.....	87.0	78.0*	91.0	84.0	82.0	75.0
H ₂ O-capacity % by weight.....	892.0	1550.0	960.0	530.0	477.0	283.0
Air dry H ₂ O-content %.....	8.5	10.6	10.0	10.0	10.0	10.0

*Low volume percentage due to air present in tissues.

These measurements were made by placing the peat samples in a zinc cylinder of 600 cc capacity. The bottom of the cylinder was closed with a wire gauze cap. The moist peat was tamped into the cylinders with as nearly uniform a stroke as possible. The cylinders were then set in a dish of water for eighteen hours, after which the cylinder was removed and allowed to drip. When all dripping had ceased, the cylinder was weighed. The peat was then removed and allowed to dry at room temperature, and again weighed. Finally it was dried at 110° C., and the absolute weight determined. As usual in such measurements, considerable irregularity was shown by the different samples, owing to the difficulty of removing the air, and of packing to the same degree. However, the figures bring out clearly the fact that sphagnum more than any other plant influences the water-capacity of a peat containing it. The eriophorum peat has a lower capacity, owing to its coarse fibrous structure. Of the series examined, the highest water-capacity was found in the cassandra zone. The effect of further decay and destruction of the plant tissue is shown by the reduction in water-capacity of the last three members of the series. The percentages are of interest in connection with the utilization of such lands for agricultural purposes, in showing the difficulty of proper drainage. It is the experience of the men who ditch these bogs that until the peat has reached the condition termed "muck" the ditches act only with extreme slowness.

Chemically, peat or humus is made up of varying quantities of several substances of a rather indefinite character, which are commonly classified among the dehydration products of the carbo-

hydrates. These bodies not only occur in nature, but may be artificially produced by the action of strong acids on starch, sugar, and cellulose. The relation of nitrogen to these bodies is still unknown. Principally on the basis of color and solubility in alkalies and acids, there are several substances distinguished. Ulmin and ulmic acid are brown, and are early products of decomposition. Humin and humic acid are black, and occur more abundantly where eremacausis has been active for a long time. Crenic and apocrenic acids appear to be further oxidation products; the former is colorless, and the latter varies from yellow to brown. *MAYER* believes these bodies to be organic nitrogen compounds (36), and on this basis *STOCKBRIDGE* (50, p. 135) explains the insolubility of peat soils and the presence of the unavailable nitrogen in peat. Beside these substances xylic, saccharic, and glucinic acids have been recognized. Although great advances have been made in soil chemics, it seems strange that the only suggestion of formulæ for these substances was made by *MULDER* in 1861 (38).

Humic acid forms water-soluble compounds with the alkalies, and to these are due largely the brown colors of the bog waters. The color may be produced by the presence of free humic acid. With the alkaline earths humic acid forms insoluble or difficultly soluble compounds. Hence there is slight chance of lime and magnesia penetrating from the surrounding soil into the peat deposits.

During the changes which the plant material undergoes in the process of peat-making there are alterations in the relative amounts of volatile hydrocarbons, fixed carbon, and ash—using these terms as in ordinary coal analyses.

	Eriophorum Stems and Leaves	Sphagnum	Eriophorum Zone Peat	Cassandra Zone Peat	Tamarack Zone Peat	Onion Marsh Muck
Volatile combustible	68.2	67.0	62.0	54.0	53.0	45.7
Fixed carbon.....	21.0	17.9	21.8	22.9	23.4	21.8
Ash.....	3.8	4.5	7.4	13.8	13.6	22.5
H ₂ O.....	7.0	10.6	8.8	9.3	10.0	10.0

The proportion of volatile combustible matter decreases regularly as the humification proceeds. The ash regularly increases, while the air-dry water content shows but slight modification.

(To be continued.)

THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY.

EDGAR NELSON TRANSEAU.

(WITH SIXTEEN FIGURES)

[Continued from p. 375.]

THE BOG AS A HABITAT FOR PLANTS.

WHEN we consider the bog as a habitat for plants, there is at once brought to mind the marked contrast between its characteristics and those of the other plant habitats of its vicinity. In both its atmospheric and edaphic conditions it is unique. The various factors entering into the plant environment will be discussed as physical, chemical, and biotic agents.

A. PHYSICAL FACTORS.—I. *Wind*.—Because of the fact that so large a number of our bogs lie in depressions surrounded by hills, the influence of the wind is somewhat lessened. It is only in the case of the larger basins that its effects become marked. It has been noted by several students of bogs (41, 5, p. 37; 59, 47) that in the region of prevailing westerly winds the greatest development of bog areas and peat deposits occurs on the western sides of lake basins. Where the deposition has taken place in a large lake basin, which is now only partially filled, we commonly find open water occurring toward the eastern side. The peat deposits at Portage, Parks, and West Lakes in the vicinity of Ann Arbor are massed on the western shores, while the eastern margins exhibit an ordinary lake beach. At the bogs north of Delhi, although nine-tenths of the original basin has been filled, the two small lakes are near the eastern margin. The facts noted in this region all favor the idea of the bog plants being unable to gain a foothold on the eastern side in the presence of wave action. The shoreward thrust of the ice is of importance at times in this connection.

Farther north in Michigan the wind frequently shows its extreme effect in these bog areas in the presence of "windfalls." Owing to the character of the substratum, such areas are more readily affected

than the forests of mineral soils. These phenomena have not been observed in any of the bogs in this vicinity.

The same statement holds for the presence of loose floating bogs which are driven about on lakes by winds (35).

2. *Temperature*.—In its temperature relations both the topography and the character of the substratum combine to influence the bog habitat. It has long been noted by agricultural writers that reclaimed bog areas are particularly subject to late frosts in the spring. One of the causes of this peculiarity lies in the fact that on clear and quiet nights the cooled air overlying elevations drains into the depressions (11). Some recent observations made by SEELEY (45) near Chicago show how effective such atmospheric drainage may be even in districts whose range of elevations amounts to but 15 feet (4.5^m). He found that the hilltop averaged, on the night of the observations, 2.5° F. (1.4° C.) higher than that of the depression while a thermometer placed 30 feet (9^m) above the hilltop averaged 8.8° F. (5° C.) above that of the "swale." On comparing the temperatures of atmospherically undrained and drained depressions with that of the hilltop, he found that the hilltop temperature was 36.3° F. when that of the drained depression was 36° F. and that of undrained 31.8° F. Here is a particular instance in which frost occurred in the undrained depression, but not in the other situations. On quiet nights low grounds in general are subject to lower temperatures than the adjoining highlands, and it is probable that these effects are more pronounced in the case of undrained depressions.

A second factor in the production of low temperatures in bogs is found in the nature of the substratum. In the spring the ice which has formed beneath the cassandra and tamarack areas melts with extreme slowness, when once the surface of the soil has been reached. This is explained by the low conductivity of the loose, partially decayed, vegetable covering, and by the shading of the plants above. For example, at First Sister Lake, in 1904, the ice had disappeared from the water surface on April 10. On April 17, with an air temperature of 10° C., the temperature of the substratum in the bog sedge zone averaged 10° C., in the Cassandra zone 6° C., in the tamarack zone 3° C., and the area of willows and sedges 8° C. Ice was found at several points among the tamaracks, an inch below the

surface. The sedge zone was covered with 1 to 3 inches (25-75^{mm}) of dark colored water. The other soils were wet, but their loose texture was effective in preventing a rise of temperature.

It follows that of the various situations in bog areas those most liable to extreme low temperatures in the spring are in the cassandra and tamarack zone. Since their maximum temperatures are considerably below those of neighboring areas, on quiet nights the plants there are but little protected by radiation from the soil as compared with plants of other situations.

In the following table it is shown that the soil temperatures of the several plant societies formed about a bog are different, and that each society has a characteristic temperature range. The records were made at First Sister Lake. The temperatures, given in °C, are averages of readings made in the second inch (25^{mm}) below the surface. The "willow-sedge" conditions correspond to those of the ordinary swamp. The "maple-poplar" is an area of these trees on the peat substratum. The "upland" is a sandy, sod-covered area 3 feet (0.9^m) above the surface of the bog. The temperatures for the most part were taken on clear afternoons about 3 p. m. when the differences are at their maxima.

Date→	April 4	April 12	April 17	April 25	April 29	May 3	May 6	May 16	May 21	May 27	June 6	June 15
Air temperature	10.5	2.0	10.0	8.5	18.0	24.0	27.0	15.0	26.0	21.0	26.0	26.0
Upland.....	11.0	7.0	10.0	10.0	17.0	20.0	23.0	16.0	20.5	21.5	25.5	26.0
Willow-sedge.....	7.0	8.0	8.0	9.0	14.5	17.7	19.5	15.0	20.0	22.0	22.0	20.5
Cassandra.....	1.5	2.0	6.0	7.5	11.0	14.7	15.5	13.0	16.5	19.0	20.0	19.5
Tamarack.....	0.0	0.0	3.0	4.5	9.0	11.7	15.0	10.6	15.0	17.0	18.0	18.0
Bog-sedge.....	9.0	8.0	10.0	9.0	18.0	10.0	22.0	16.0	20.0	23.0	24.0	23.0
Maple-poplar.....	7.0	8.0	8.0	8.0	15.0	18.0	19.0	15.0	16.0	15.0	17.0	16.5

In the accompanying diagram (*fig. 5*) it will be seen that the upland, bog-sedge, and willow-sedge soil temperatures do not deviate widely from those of the air, while the temperatures of the cassandra and tamarack areas range considerably lower. The high temperature of the bog-sedge zone finds its explanation in that the brown bog water overlying its surface absorbs heat. I have tested this point many times in various bogs and have always found such bog water to have a higher temperature than that of the saturated substratum adjoining it. In its ability to absorb heat rays it approaches that of drained sand. Its range, however, is much less and it retains its

heat for a longer time. Consequently on cloudy days and following a sudden lowering of the air temperature, the surface bog-water temperature stands above that of the drained and undrained soil.

When we compare the effects of loss of heat from a free water surface and a saturated humus soil surface due to evaporation, there

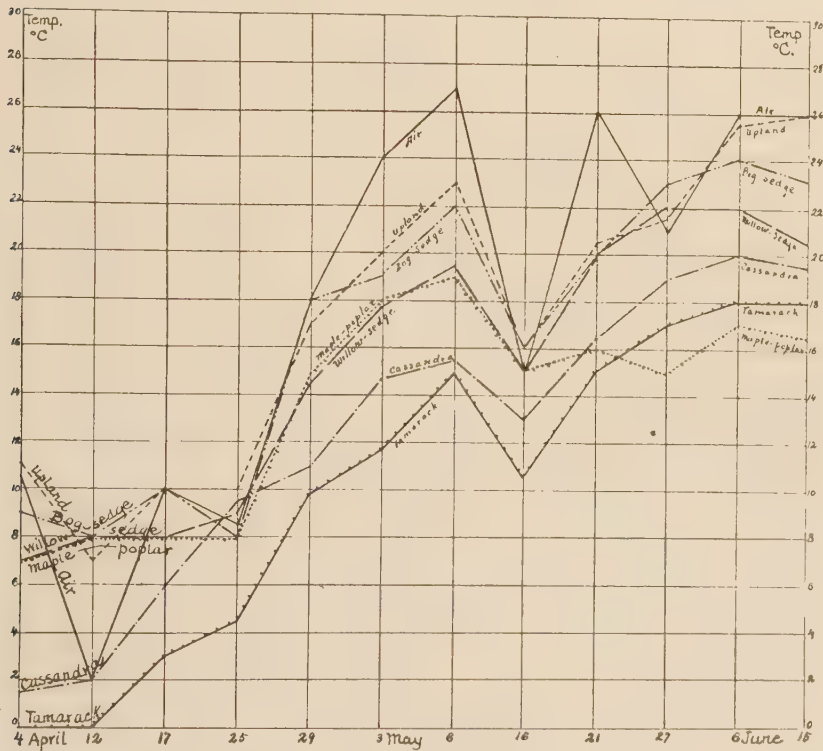


FIG. 5.—Diagram showing temperatures of the air and the substrata in the several plant societies.

is a marked difference due to their specific heat. The humus will be cooled more rapidly by the evaporation of a given amount of water. Where so large an evaporating surface is exposed to the air as in the case of a sphagnum-covered area the loss of heat by this process is most effective in preventing the penetration of heat below the surface.

In the case of drained soils, the most effective agent in raising

the temperature of the subsoil is that of percolating water which has been warmed at the surface of the soil. Because of the high water-table and the stagnant condition of the underground water in bog areas, this source of heat is relatively unimportant.

The effects of these factors, resulting in low soil temperatures, are far-reaching. As compared with well-drained soils, chemical action is retarded, the rate of diffusion, solution, and osmosis is greatly reduced, and the conditions for the existence of soil bacteria made unfavorable. Plants which can successfully compete for the occupancy of such areas must be able to withstand low temperatures and late frosts. The difference between the temperature of the air and that of the substratum favors plants having a low transpiration ratio.

However, in so far as the region of southern Michigan is concerned, the temperatures prevailing in bog areas do not seem to be adequate to account for the presence of the bog plants or their xerophilous structures. It is to be noted that with the leafing-out of the trees, about May 27, the temperature of the maple-poplar substratum falls below that of the tamarack. But that the soil temperature is one of the factors entering into the problem of competition between species there can be little doubt. It is probable also that in the region of optimum conditions for bog plants the conditions which occur here only in the spring are prolonged through the summer. That is, the difference between air and substratum temperatures is more marked, and is a powerful factor in the selection of plants for bog areas and in the production of xerophilous structures.

3. *Texture*.—This property of the substratum has already been referred to in connection with the genetic changes in peat. The sedge zone is developed upon a raft of interwoven rhizomes and roots. It is a coarse meshwork; but since it lies at or below the surface of the water, its texture is of slight importance except as a means of mechanical support. As the bog develops, the admixture of moss and shrub debris brings about the formation of a rather compact peat, overlaid by a stratum of loose material. In some cases, as at Delhi and Oxford, 45 miles (72^{km}) northeast of Ann Arbor, the living sphagnum makes up the bulk of this loose covering. Usually the water level lies just beneath it. As a consequence, this covering becomes the

principal seat of root activity. The small, fibrous roots of cassandra, andromeda, and the cranberry penetrate it in all directions, and it is from the water which is held among this moss and débris that they derive their water and mineral salts.

The substratum beneath the tamaracks is also covered by a loose litter of leaves and twigs, with more or less moss. Depending upon the height above the ground water level, this surface layer is of greater or less thickness. In it occur the wide-spreading roots of the tamarack. During summer and autumn it furnishes admirable conditions for the growth of fungi, and it is penetrated everywhere by their mycelia.

When bog land is cleared, the decomposition of the surface layers is very rapid, owing to exposure to sunlight and higher temperatures. If the water-table is maintained near the surface, sedges and willows develop as the covering. The annual increment of plant material is often decreased, and in place of the fibrous and porous substratum there is produced a black, close-textured, and plastic muck.

If ditching and draining are added to clearing, the summer drought dries the surface layer so thoroughly that it often becomes the habitat for many dry-ground weeds. Decay progresses in moist weather under the influences of the higher temperatures resulting from increased absorption of the sun's energy by the dark colored soil.

4. *Mechanical properties.*—Bog soils in general do not afford as good a foothold for the development of tree species as do the mineral soils. On account of the high water-table, the roots of the plants are not able to penetrate to a depth of more than a few inches. The roots of the tamaracks spread out in all directions from a flat trunk base, and upon the size and strength of these horizontal roots depends the tree's ability to withstand mechanical strains tending to displace it. There can be no doubt but that, in the thick groves in which the tamarack occurs, the interweaving of the roots from adjacent trees becomes of mutual advantage, in so far as the roots function as hold-fast organs.

5. *Diffusion properties.*—A most important soil property relates to the diffusion of mineral salts. This becomes of especial significance in saturated stagnant substrata. The mineral salts must be distributed to the roots mainly by diffusion, for lateral drainage

and percolation are at a minimum. It is well known that when salt solutions are passed through soil, much of the salt is retained by absorption. The relative amount is greatly increased in the case of humous bodies. BLANCK (4) has further found that the diffusion of water in humus soils is decreased by the presence of acid humus compounds, and that this may be corrected by the addition of a neutralizing agent, such as lime. All analyses of peat show how little of this mineral matter has been derived from the adjacent soils. It is only in the case of samples taken from the bottom or edge of a bog that the mineral salts cannot be accounted for by the amount derived from the decay of the plant material, and that obtained from the atmosphere.

6. *Water-capacity*.—The high water-capacity of peat has already been noted. In relation to plant growth, it is detrimental in that it prevents proper aeration of the substratum (39, p. 346). So far as the diffusion of gases is concerned, such substrata are less favorable than a free water surface. King (29, p. 161), in speaking of sand and clay soils whose water-capacity is only 17.5 to 32.2 per cent. by weight, says that 30 to 40 per cent. of their saturation amounts must drain away before the soil can contain air enough to maintain the respiration of roots and germinating seeds. As compared with a free water surface, saturated humus cannot admit oxygen as freely, owing to the large part of the surface actually occupied by the humus (29, p. 239). In a chemical way it is still more effective, as will be noted later.

7. *Osmotic pressure*.—The osmotic pressure of bog waters has been found to be about the same as that of ordinary lakes and rivers.³ They are approximately equivalent to a 0.1 to 0.5 per cent. normal Knop's solution. They indicate quite certainly that bog plants do not owe their distribution and their peculiar structures to a high osmotic pressure of the bog water.

³ Four samples of bog water from this vicinity were tested by Dr. B. E. LIVINGSTON, of the University of Chicago, and found to have the following pressures in millimeters of mercury at 25° C.:

First Sister Lake, Sample A	50.0742
First Sister Lake, Sample B	49.0593
West Lake, Sample A	100.1484
West Lake, Sample B	150.2226
Lake Michigan water	100.1484

See 33.

B. CHEMICAL FACTORS.—I. *Ground water*.—The ground water of the Huron basin derives its mineral constituents from the glacial drift. The following analyses show the character of the solution. Quantities are expressed in parts per million (31).

	CaCO ₃	CaSO ₄	Fe ₂ O ₃	MgCO ₃	K ₂ SO ₄	SiO ₂	NaCl	Na ₂ CO ₃	Na ₂ SO ₄	Organic and volatile	Total mineral matter
Ann Arbor, University well.	178.00		3.99	60.58	6.78	7.30	4.48	1.52	5.07	3.85	267.72
Ann Arbor, spring.....	228.00		6.43	89.36	5.31	9.20	4.88	0.42	9.71	25.00	353.31
Ypsilanti, water works....	289.00	39.00	21.00	100.00		14.00	35.00			71.00	498.00
Ypsilanti, well.....	156.00	223.00	Tr.	109.00		18.00	62.00	17.00		14.00	585.00
Ann Arbor, creek.....	128.00	99.00	Tr.	83.00		25.00	15.00 (NaK)	25.00 (NaK)		14.00	375.00

It is to be noted that they are all high in calcium and magnesium content, and under favorable drainage conditions contain sufficient minerals for plant growth. The ground water is of especial importance in the early stages of bog development, when the sedge and aquatic vegetation is dominant. With the further development of the sedge zone and the formation of a thick peat deposit, its relation to the vegetation becomes of less moment. There is a notable difference between the total mineral content of bog water and that of the soil waters adjoining. In the above table the total mineral content of the ground water varies from 267.7 to 585 parts per million. In three analyses of the bog water at the First Sister Lake I found the total mineral content to vary from 89.9 to 219 parts per million, the highest figure being that for the sample obtained near the margin of the tamaracks, *i. e.*, nearest the mineral soil.

The absence of sphagnum from certain bogs has been explained by the presence of calcium salts (15, p. 23, 16). In order to test this point, I have cultivated the species found in this vicinity in tap water and in a saturated solution of CaCO₃, and have found no detrimental effects due to calcium. The experiments will be discussed later. I further found that the ash of sphagnum growing at First Sister Lake contained 18 per cent. of CaO. It would seem, therefore, that, in so far as this vicinity is concerned, the presence of calcareous waters will not explain the absence of species of sphagnum.

2. *Acidity*.—Much stress has been laid by various authors, following SCHIMPER (44, pp. 6, 18, 124), upon the acidity of the bog water as a factor in the bog habitat. In order to get a quantitative statement of the acidity for the bogs of this vicinity, a number of 50°c samples have been titrated with an $n/100$ solution of potassium hydrate Phenolphthalein was used as an indicator. The results show an acidity varying from .00015 to .00258 normal acid.⁴ The lowest values are found in the areas occupied by bog sedges and by swamp plants, and they are practically the same. The areas occupied by cassandra and sphagnum have a somewhat greater acidity. The highest percentages are found beneath the tamaracks. The explanation of these variations in acidity is suggested by the tests, made from time to time, of the water in my experimental cultures. I found that the acidity of the water increased slowly in the undrained peat substratum cultures (see experiments). The increase was small in the case of the warm cultures, but quite notable in the case of the cold undrained substratum. On exposure to air in the water cultures, and in bottles, the acidity very slowly decreased, the decrease being greatest in the case of the water which was kept warm. This is probably due to increased oxidation. These relative amounts of acid, it will be seen, may be correlated with the temperatures in the several plant societies of the bog, the lowest temperatures corresponding to the highest percentages of acid. This suggests the probability that the acidity of the bog substratum increases farther north.

On allowing open dishes of bog water to stand for some time, I found that the evaporation was not sufficient to raise the acidity of the water, oxidation apparently being more rapid than concentration of the solution.

There is no apparent relation between color and acidity, although the lightest colored solutions usually show but slight acidity. This seems to indicate that only a part of the color is produced by free humus acids, the remainder by humates of the alkalies.

⁴ Following are the determinations expressed in fractions of a normal acid solution:

First Sister Lake: sedge zone, .00066, .00094; cassandra zone, .00152, .00119; tamarack area, .00165, .00179, .00227, .00258; willow-sedge area, .00089, .00072.

Chelsea: ditches, .00086, .00015, .00043, .00019, and .00029.

Delhi: tamarack area, .00146, cassandra zone, .00117.

Oxford: cassandra zone, .00094.

The effect of acidity upon cultivated plants has been investigated in this country especially at the Rhode Island Agricultural Experiment Station, under the direction of Professor H. J. WHEELER. The experiments have been conducted upon "acid upland soils" (60), and numerous reports have been published. These experiments involved a great variety of plants and were carried on under natural field conditions. The areas planted for comparison had their acidity neutralized by the addition of CaCO_3 . The plants which were favored by the liming include the orange quince, black Tartarian cherry, Japan plum, *Tilia americana*, *Ulmus americana*, rhubarb, Australian salt-bush, hemp, barley, oats, onions, *Anthoxanthum odoratum*, *Poa pratensis*, *Festuca ovina*, *Holcus lanatus*, *Festuca elatior*, *Alopecurus pratensis*, etc. Plants which appear to be adapted to the acid soil conditions include cranberry, blackberry, raspberry, sheep sorrel, cow-pea, flax, corn, lupine, and soja bean. It would appear, then, that the acidity of the soil solution is unfavorable for the growth of some plants, and that it is a factor in the selection of species for acid soil conditions.

3. *Food material.*—As to the presence of plant food materials in the bog soil there is an agreement among all the analyses that have been made.⁵ The soils are unusually rich in nitrogenous materials, some analyses showing three times as much as good upland soils. But in the slow decay of the vegetable matter the nitrogen remains bound up in organic compounds and is unavailable for the growing plants. This is confirmed by experimental tests in which nitrogen was directly applied, and by tests in which the conditions were modified so as to permit the action of nitrifying bacteria. In such cases crops were produced when the untreated humus produced none.

Under natural conditions the growth of the nitrifying bacteria in bog soils is almost impossible. Three factors work against their activity: (1) the acidity of the soil solution; (2) the lack of oxygen due to high water content; (3) the lower temperature. It has been found that the optimum temperature for these bacteria is 98° F. (36.6° C.), and that their activity is very slight at 50° F. (10° C.)

⁵ Analyses of Wisconsin soils. Ann. Rept. Wis. Agric. Exper. Sta. 13: 304. 1896. See also 27, p. 12; 23; 22, p. 276; 30; 48, p. 234; 12, p. 39; 14.

(3). Furthermore, it has been shown that when soil rich in nitrogen is saturated with water so as to exclude free oxygen, denitrification takes place and nitrogen gas is set free (29, p. 115).

The phosphoric acid content is comparable with that of the best soils, and it is at least partially in a condition for plant use.

The potassium content is very low. Analyses and the results of agricultural experiments show that in order to produce crops this substance must be added, and preferably in an alkaline form. Inquiry among the owners of onion marshes in this vicinity confirms the need for potassium in local bog soils.

The amount of calcium present is reported as equal to that of the best upland soils. But it is probable that as it exists under natural conditions in bogs it is bound up largely in insoluble humates. Under the influence of oxidizing processes it would become available to the plants at the surface.

When we consider the conditions under which the various plant societies in our bogs exist and their competition with one another, there can be little doubt but that the substratum varies in each case as to its chemical composition. That the societies may be classified on a physiographic basis is certain, but how to determine the chemical factors accompanying each physiographic change is an unsolved problem. The ordinary methods of analysis give us the minerals present, but tell us little about their form and availability for plant assimilation. The colorimetric methods for determining the quantity of mineral salts present in bog water are mostly open to objection. The ease with which the humous bodies of the bog water are decomposed render their quantitative estimation by present methods of little value. Yet it seems probable that work upon the chemistry of humus and humous compounds must result in data valuable alike to the ecologist, the forester, and the agriculturist.

C. BIOTIC FACTORS.—The interrelations of the bog species will be discussed in connection with their other ecological characters. It will be sufficient to mention here that they are with a few exceptions light-demanding forms. Consequently, size and ability to produce shade are the important factors in their competition with one another.

A second element enters into this problem of the struggle between

species near the borders of the area of geographic distribution of the bog plants, viz., climate. The bog plants of this vicinity come into conflict with species whose range is either more nearly continental or more southern. That the climatic and edaphic conditions of this region are at present unfavorable to the successful competition of the bog species with swamp species is evidenced wherever the bog conditions have been disturbed. That the reverse is the rule in eastern Canada has been shown by GANONG (18, p. 178). The tenacity with which species, whose multiplication is principally accomplished by vegetative means, hold an area under complete control is apparent to any who have studied the vegetation of lake shores. It is just as strongly marked in the case of the herbaceous and shrubby bog vegetation. When we examine the chemical and physical data, now at hand, concerning the soils occupied by bog and swamp plants respectively, the conclusion must be that they are wholly inadequate to account for the difference in vegetation. The forester lays stress upon the fact that trees cannot gain a foothold on areas now covered with a grass turf because of the difficulty of the seedlings getting started. The bog societies form an equally compact plant growth, and their preservation in this region would seem to be dependent upon analogous factors.

III. The bog-plant societies.

The following descriptions of local bog areas occurring in the Huron valley aim not only to present lists of plants found in this vicinity, but to show their natural associations. The order in which the areas are described corresponds to the relative amount of filling which has occurred in the several basins. To a certain extent this order is genetic, yet there can be little doubt but that many arctic plants which were concerned in the pioneer stages of our mature bogs are now extinct. If we accept the areas at West and First Sister Lakes as representing bogs in youth, maturity may be illustrated by the original vegetation of the bog on Carpenter's road. The Chelsea area defines that stage beyond the climax, when the conditions inaugurated by cutting, firing, and ditching have destroyed the original tamarack forest, and in its place has come a rude mixture of bog relicts and arborescent weeds.

WEST LAKE.

This lake, situated three miles north of Chelsea (Sec. 30, Dexter Tp.), is also known locally as Johnson's Lake. In area it is slightly more than a fourth of a square mile (65 hectares). The margin of the lake originally extended a half mile (0.8^{km}) farther west and southwest. This part is now occupied by a partially floating bog. The north, south, and east shores are sandy and low. Patches of bulrushes and water-lilies occur here and there over the lake and show its generally shallow character. Toward the east there is a narrow swampy outlet by which its water after a long and circuitous route reaches the Huron River. There are no streams tributary to the lake. The basin lies near the southeastern margin of the interlobate moraine, and is bounded on the north and south by hills 60 to 80 feet (18-24^m) in height. Not all of the original extension to the southwest has been filled by peat; two small areas of open water still remain.

The shores, with the exception of the western side, support a vegetation similar to that of many lakes in this region. Three societies of plants may be distinguished.

Aquatics.—The most abundant plants are *Scirpus lacustris*, *Castalia tuberosa*, and *Sagittaria rigida*. These occur not only along shore, but in shallow water throughout the lake. Associated with these are *Naias flexilis*, *Brasenia purpurea*, *Potamogeton heterophyllus*, *Chara* (sp.), *Spirodela polyrhiza*, *Vallisneria spiralis*, *Scirpus americanus*, and *Decodon verticillatus*.

Sedge-grass society.—Very near the north, south, and east shores occur a great number of species of grass-like plants. Their associations vary greatly at different parts of the shore line. The dominant forms are *Carex filiformis*, *Panicularia nervata*, *Eleocharis palustris*, *Carex teretiuscula*, *C. Muskingumensis*, *Dulichium arundinaceum*, *Panicularia Canadensis*, *Dryopteris Thelypteris*, and *Scutellaria galericulata*. Among the species of secondary importance are *Onoclea sensibilis*, *Carex riparia*, *C. stipata*, *C. hystricina*, *C. interior*, *Spartina cynosuroides*, *Typha latifolia*, *Iris versicolor*, *Lobelia Kalmii*, *Comarum palustre*, *Lycopus americanus*, and *Eupatorium maculatum*. Closely associated with these plants are the seedlings of the shrubs and trees which make up the next society.

Willow-maple society.—The shrub and tree border is composed,

for the most part, of *Salix Bebbiana*, *S. discolor*, *S. sericea*, *Cornus candidissima*, *Acer rubrum*, and *Ulmus americana*. Beside the many plants of the sedge-grass society which remain as relicts, the accessory species include *Rosa Carolina*, *Impatiens biflora*, *Sambucus pubens*, *Spiraea salicifolia*, *Prunus serotina*, *Quercus alba*, *Q. velutina*, and *Opulaster opulifolius*. These trees grade into the forests of the upland and establish a natural order of succession.

An interesting comparison is afforded when we note the species dominant along the western or bog margin. Here the outer zone of aquatics is made up of the same species, but this substratum is a floating raft constructed by the plants themselves. Without again enumerating the species, we pass to the society which closely follows their development.

Bog-sedge and shrub society.—This society forms a very complex growth, averaging 50 feet (15^m) in width. On the lakeward side are the aquatics; on the other, the growth of tamaracks. The sedges and shrubs are not separable, as in many other localities. *Carex filiformis* is by far the most important plant in the society. Its vigorous production of rhizomes and roots especially fit it for the position which it occupies. Certain other plants are locally abundant and of great consequence. These include *Dryopteris thelypteris*, *Menyanthes trifoliata*, *Eleocharis palustris*, *Comarum palustre*, *Sagittaria latifolia*, *Eriophorum polystachyon*, *Carex teretiuscula*, *Typha latifolia*, *Salix myrtilloides*, *S. candida*, *Betula glandulosa*,⁶ *Oxycoccus macrocarpus*, and *Andromeda polifolia*. As accessory species may be mentioned *Salix discolor*, *S. Bebbiana*, *Cicuta bulbifera*, *Cardamine pratensis*, *Chamaedaphne calyculata*, *Campanula aparinoides*, *Rumex Britannica*, *Epilobium adenocaulon*, *Asclepias incarnata*, *Pogonia ophioglossoides*, *Blephariglottis blephariglottis*, *Limodorum tuberosum*, *Marchantia polymorpha*, *Aulacomnium palustre*, *Sarracenia purpurea*, *Drosera rotundifolia*, *Boehmeria cylindrica*, *Carex comosa*, *C. hystricina*, *Cornus stolonifera*, *Parnassia caroliniana*, *Viola blanda*, and *Penthorum sedoides*. Here and there occur young tamaracks which by their growth inaugurate the next society.

Tamarack society.—As development proceeds, the shrubs and

⁶ The form found here and at Delhi corresponds more closely to this species than to *B. pumila*, but its characters are intermediate.

herbs gradually are superseded by a growth of *Larix*. This society has been much disturbed by lumbering, and a large part of the original area has been cleared. But there is good evidence to show that the part of the basin filled with peat formerly supported a dense covering of tamaracks. Where best developed and least disturbed, it shows an undergrowth of *Vaccinium corymbosum*, *Aronia nigra*, etc. As the other species are practically the same as at the lake to be described next, they need not be enumerated here. In contrast with most of the areas studied, the almost complete absence of sphagnum is worthy of note. It is also important that the absence of any gradation between the forest societies of the upland and of the bog be kept in mind.

On this lake, then, there are two divergent series of plant societies. Starting with practically the same species, the one series leads us on mineral soil through willows, maples, and elms to the oaks of the surrounding forests; the other, owing to the development of a floating substratum, involves a very different set of shrubs and ends with the tamarack. The former series therefore more closely approximates the climatic type, while the latter is dependent upon edaphic factors.

FIRST SISTER LAKE.

This lake and its accompanying bog are located three miles west of Ann Arbor in a glacial drainage valley. Its origin is probably connected with the melting of a mass of stagnant ice after the abandonment of the valley by glacial drainage. The surrounding and underlying soil is a sandy gravel. At least a part of the western side presents an original tamarack bog vegetation, and it is particularly interesting in showing the results of competition between bog plants and those of other habitats (*fig. 6*). The vegetation in general presents a different phase of the bog societies, as compared with West Lake. Especially to be noted are the dominance of *cassandra* and sphagnum in the shrub zone, the absence of cattails and swamp loosestrife as important members of the outer margin. The tamarack zone is also raised somewhat more above the water level.

Aquatics.—With the exception of the shallow-water forms, the lake is almost free of higher vegetation. *Potamogeton lucens* and *P. zosterifolius* occur sparingly. About the margin, however,

Nymphaea advena is of great importance. It forms an almost continuous zone 10 to 25 feet (3–7.5 m) in width. Patches of *Castalia tuberosa* and *Brasenia purpurea* occur. This arrangement in groups seems to be connected with their rapid multiplication by rhizomes. *Typha latifolia* occurs in a small area at the north end of the lake. *Ceratophyllum demersum* and *Najas flexilis* occur as secondary species.

Bog-sedge society.—*Carex filiformis*, *C. oligosperma*, *Eleocharis palustris glaucescens*, and *Eriophorum polystachyon* are the primary factors in the formation of this zone. *Carex riparia* has gained a foothold at the north end of the lake, where muskrats have been active in destroying the original sedge zone. *Dryopteris thelypteris*, *Onoclea sensibilis*, *Juncus effusus*, *J. canadensis*, *Comarum palustre*, *Salix myrtilloides*, *Dulichium arundinaceum*, *Equisetum fluviatile*, *Bidens trichosperma tenuiloba*, *Menyanthes trifoliata*, *Viola blanda*, and *Eriophorum virginicum* occur as accessory plants. The great majority of these plants aid in the construction of the substratum by their roots and root-stocks.

Here and there among the sedges occur the forerunners of the shrub society. Among the very first to gain a foothold are the sphagnums. These build small tufts of great compactness, and gradually overcome the sedges. The rootstocks of the cassandra also send up shoots and prepare the way for another vegetation form. *Oxycoccus macrocarpus* and *O. Oxycoccus* both occur at intervals in this zone.

Cassandra-sphagnum society.—Beyond the sedge zone the vegetation is no longer arranged zonally. Conditions have been so much

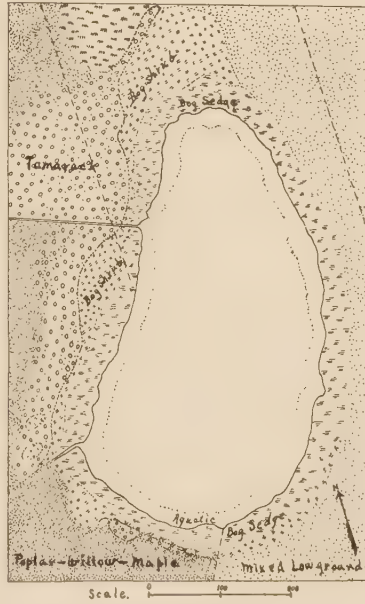


FIG. 6.—First Sister Lake.

disturbed that on the western side the area of cassandra-sphagnum dominance is very irregular. On the eastern side this plant society is in the last stage of its existence. The intimate association of *Chamaedaphne calyculata*, *Sphagnum cymbifolium*, *S. subsecundum*, and *S. recurvum* is well illustrated here. The plants occupy the whole of the territory where they flourish. The other species are decidedly secondary. It is to be further noted that in the competition with the sedge species these plants actually override them, and only an occasional *Eriophorum virginicum* survives. The water-conserving properties of the sphagnum are too well known to need description here. But the mutual advantage of the cassandra-sphagnum combination is worthy especial note. The former by its numerous branches furnishes a framework which aids in the upbuilding of the moss and in shading. The sphagnum, on the other hand, furnishes a moist cover in which the conditions for the shrub are most favorable.

The accessory species include the moss, *Aulacomnium palustre*; the herbs, *Drosera rotundifolia*, *Arethusa bulbosa*, *Habenaria lacera*, *Sarracenia purpurea*, *Pogonia ophioglossoides*, *Limodorum tuberosum*, *Viola blanda*, *Osmunda regalis*, *Campanula aparinoides*, *Scutellaria galericulata*; and the shrubs, *Andromeda polifolia*, *Betula pumila*, *Oxycoccus macrocarpus*, *O. Oxycoccus*, *Aronia nigra*, and *Ilicioides mucronata*.

Tamarack society.—Among the cassandra occur many young tamaracks, and these by their development come to overshadow the shrubs and form the tree society of the bog. The dead remnants of the cassandra mounds make up a large part of the floor beneath them. The species of secondary importance are *Ilicioides mucronata*, *Aronia nigra*, *Chamaedaphne calyculata*, *Osmunda cinnamomea*, *O. regalis*, *Dryopteris spinulosa intermedia*, *D. cristata*, *Polytrichum juniperinum*, *Plagiothecium denticulatum*, *Thuidium recognitum*, *Aulacomnium palustre*, *Marchantia polymorpha*, *Sphagnum cymbifolium*, *Boletinus porosus*, and *Thelephora intybacea*.

The tamarack zone has been much disturbed by clearing and burning. At the present time a large part of the area on the southwest side is dominated by other tree species. Some of the plants of the clearing have spread into the pure tamarack growth.

Poplar-willow-maple society.—Where the original conditions have been disturbed and a second growth allowed to come in, *Populus tremuloides*, *Salix sericea*, *Salix discolor*, and *Acer rubrum* have obtained dominance. Where groups of the more mature poplars occur there is scarcely any undergrowth. Elsewhere the following plants occur: *Ilicioides mucronata*, *Salix Bebbiana*, *Sambucus pubens*, *Amelanchier oligocarpa*, *Aronia nigra*, *Rubus nigrobaccus*, *Cornus stolonifera*, and *Rubus strigosus*. These form a dense mixed association, with but slight reference to substratum conditions. The smaller species present are *Adicea pumila*, *Osmunda cinnamomea*, *Rosa Carolina*, *Onoclea sensibilis*, *Epilobium adenocaulon*, *Spiraea salicifolia*, *Dryopteris thelypteris*, *Verbena hastata*, *Solanum dulcamara*, *Polygonum sagittatum*, *Spiraea tomentosa*, *Geum rivale*, *Polygonum hydropiperoides*, *Ribes floridum*, *Ribes oxyacanthoides*, *Rumex Britannica*, *Impatiens biflora*, *Viola blanda*, *Osmunda regalis*.

On the southeast side of the lake and on the north, conditions have been still more interfered with, and there is now a mixed growth of bog and low-ground plants, which represent stages in the decline of the bog flora and the advent of swamp plants. The tallest forms are willows and clumps of mountain holly. For convenience only, the plants may be enumerated together under the following title:

Mixed low-ground society.—The dominant plants are *Salix sericea*, *S. discolor*, *Spiraea salicifolia*, *Poa flava*, *Solidago serotina*, *Chamaedaphne calyculata*, *Oxycoccus macrocarpus*, *Aster Novae-Angliae*, and *Rosa Carolina*, *Epilobium adenocaulon*, *Aronia nigra*, *Andromeda polifolia*, *Rubus strigosus*, *Dryopteris thelypteris*, *Scutellaria galericulata*, *Juncus effusus*, *Koellia virginiana*, *Sambucus canadensis*, *Geum rivale*, *Osmunda regalis*, *Scirpus cyperinus*, *Galium aparine*, *Homalocenchrus oryzoides*, *Juncus tenuis*, *Asclepias incarnata*, *Salix Bebbiana*, *Eupatorium perfoliatum*, *Gentiana Andrewsii*, *Lycopus virginicus*, *Osmunda cinnamomea*, *Cornus stolonifera*, *Carex riparia*, *Viola blanda*, *Sarracenia purpurea*, *Dryopteris cristata*, *D. spinulosa intermedia*, and *Triadenum virginicum* also occur.

The last two societies are found upon a black peat substratum which is more thoroughly decayed than in other parts of the bog.

Acidity tests show that the relative acidity is less than in the case of the cassandra-sphagnum and tamarack societies. The soil temperature also runs somewhat higher as noted elsewhere.

The First Sister Lake may be said to be dominated by three well-marked bog and two mixed societies in which bog and swamp species are brought into competition. The result can be foretold with considerable certainty. The bog vegetation will sooner or later be replaced by the swamp species.



FIG. 7.—Delhi bog and adjacent topography. Scale 1:95,000 ($\frac{3}{8}$ inch = 1 mile).

BOG NORTH OF DELHI.

Two miles north of Delhi occurs an extensive bog which was formerly a mile and a quarter (2 km) long by a half mile wide (0.8 km) at its broadest part (fig. 7). The southwestern third has been cleared and is in part under cultivation. The eastern and northern parts have been somewhat interfered with by the cutting of timber, but areas occur which have been but little disturbed by these influences. Near the eastern margin are two small lakes, the last remnants of the larger lake which must have occupied this territory in early postglacial times. The basin is located in a clay moraine of the Erie ice-lobe, and probably owes its origin to unequal deposition by the glacier.

The plant societies found about the southeastern lake will give an idea of the whole vegetation (fig. 8).

Aquatic society.—The aquatic vegetation is represented almost wholly by the yellow water-lily, *Nymphaea advena*. This plant forms a broader zone completely encircling the lake and varying from 5 to 10 feet ($1.5\text{--}3\text{ m}$) in width. Accompanying it occur *Brasenia purpurea*, *Ceratophyllum demersum*, *Lemna minor*, and *Spirodela polyrrhiza*.

Typha-cassandra-sphagnum society.—On the floating margin of the bog substratum occurs a zone which partially encircles the lake. Near its outer edge *Typha latifolia* is the characteristic plant, but in certain places it is wanting or extends the full width of the zone. *Chamaedaphne calyculata*, *Sphagnum cymbifolium*, *S. subsecundum*, *S. recurvum*, *Carex filiformis*, *Eriophorum polystachyon*, and *Salix*

myrtilloides are the most frequent plants. The accessory species include *Carex oligosperma*, *Menyanthes trifoliata*, *Comarum palustre*, *Triadenum virginicum*, *Osmunda regalis*, *Onoclea sensibilis*, *Rumex Britannica*, *Asclepias incarnata*, *Viola blanda*, *Cicuta bulbifera*, *Galium Aparine*, *Scutellaria galericulata*, *Rhus Vernix*, *Dulichium arundinaceum*, *Oxycoccus macrocarpus*, *Hypnum cordifolium*, *Hypnum Schreberi*, *Aulacomnium palustre*, and *Mnium*.

Vaccinium-aronia society.

—Forming a narrow transition society between the low shrub zone just described and the tree society, occurs a dense line of tall shrubs. The dominant species are *Vaccinium corymbosum*, *Gaylussacia resinosa*, *Aronia nigra*, *Ilicioides mucronata*, *Betula glandulosa*, and *Prunus serotina*. The other species present are *Acer rubrum*, *Sambucus pubens*, *Osmunda cinnamomea*, *Salix discolor*, *S. Bebbiana*, *Spiraea salicifolia*, *Ilex verticillata*, *Rosa Carolina*, *Sarracenia purpurea*, *Andromeda polifolia*, *Calamagrostis canadensis*, and *Eleocharis palustris glaucescens*. These shrubs border the tamaracks and to varying distances extend back among them.

Tamarack-birch society.—*Larix laricina* and *Betula lutea* must have made up the great bulk of the original forest which occupied this area. The relative abundance of the latter has probably been increased by the cutting of the tamarack. The next most important tree is *Acer rubrum*, which occurs scattered throughout, but is especially abundant near the northeast side. Where isolated trees have been removed, the shrubs which occur among the undergrowth have

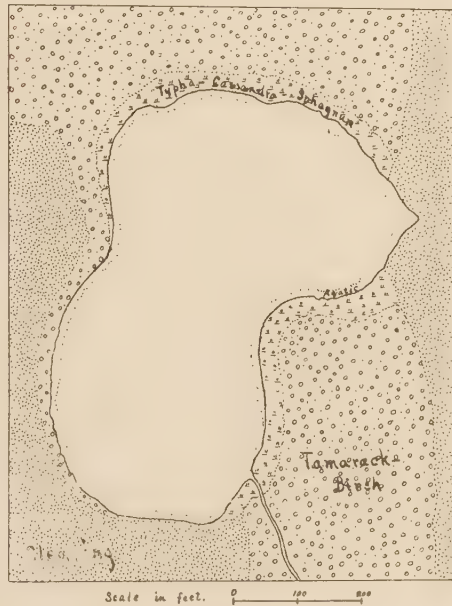


FIG. 8.—Portion of Delhi bog.

made a rapid growth. Throughout the forest area are patches in which *Aronia nigra*, *Vaccinium corymbosum*, and *Illicioides mucronata* stand so thickly as to be almost impenetrable. Where the forest has been but slightly disturbed and the tamaracks are more or less scattered, one finds a deep carpet of sphagnum with slender stems of *cassandra*, *andromeda*, and *Eriophorum virginicum* rising through it. Clusters of *Sarracenia purpurea* are common. The other plants found in this society are *Trientalis americana*, *Unifolium canadense*, *Coptis trifolia*, *Rumex Acetosella*, *Rubus strigosus*, *Dryopteris spinulosa intermedia*, *Osmunda cinnamomea*, *Viola blanda*, *Impatiens biflora*, *Solanum dulcamara*, *Thelephora intybacea*, *Polytrichum juniperinum*, *Sambucus pubens*, *Agrostis alba*, *Blephariglossis lacera*, *Cornus candidissima*, and *Cicuta maculata*.

Clearing society.—Surrounding the forest on the east, south, and west sides is a large area, in part dominated by sedges and grasses, and in part by a typical “slashing.” It is impossible to characterize this plant association by any particular species. All that have been thus far mentioned occur in scattered clusters, the proportions and dominant plants varying from one locality to another. The notable facts are that on the east side *Carex teretiuscula*, *C. vulpinoidea*, *C. riparia*, *C. filiformis*, *Scirpus cyperinus*, *Calamagrostis canadensis*, *Aster Novae-Angliae*, *Eupatorium perfoliatum*, and *Aster junceus* have become the most abundant forms. To the west of the lake these plants are present, but the taller shrubs are in control. *Salix discolor*, *Cornus stolonifera*, *Salix Bebbiana*, *S. sericea*, and many others already mentioned as occurring among the tamaracks are present.

The second lake and the more northerly one is bordered by an exceedingly narrow zone of low-growing plants. The dominant species are *Decodon verticillatus* and *Typha latifolia*. *Chamaedaphne calyculata*, *Carex riparia*, *Panicularia canadensis*, and *Bromus Kalmii* are of secondary importance. The trees come almost to the water's edge. The proportion of red maples among the tamaracks and birches is considerably greater than in the vicinity of the other lake. Otherwise the tree society is essentially the same.

We have illustrated, then, in the bogs at West Lake, First Sister Lake, and Delhi, three stages in the filling of old lake basins. We

have seen that, although there are minor variations in the species present, all of the bogs show a series of bog-sedge, shrub, and conifer societies which are genetically related. In the Delhi bog the filling is almost completed. In the bog about to be described we find this process finished, and what was formerly a ring of bog-sedges surrounding an open lake has become an irregular disk forming the central plant society of the area.

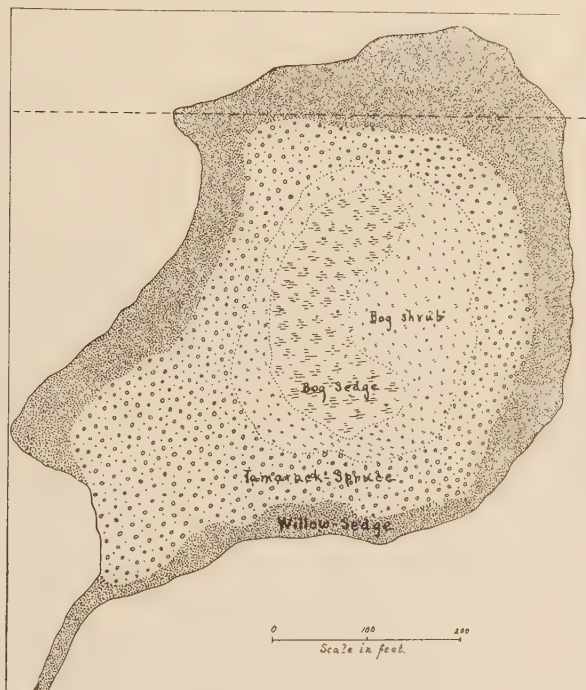


FIG. 9.—Bog near Oxford, Oakland county.

BOG NEAR OXFORD, OAKLAND COUNTY.

Near the northeast corner of Sec. 31, Oxford Tp., there is a bog (*fig. 9*) covering about 4.5 acres (1.8 hectares). Although it lies a few miles beyond the real boundary of the Huron River basin, it is included because it exhibits a flora somewhat different from the other areas, and may be considered as a near approach to the type of bogs occurring farther north. The basin is a depression in the outwash sands and gravels of the interlobate moraine. It is sur-

rounded by hills 25 to 30 feet (7.5-9^m) in height above the bog level. During wet weather it has a shallow outlet to the southwest. The land surrounding it has all been cleared and is now under cultivation. As shown by other timber areas in the vicinity, it is probable that the original upland timber was made up in part of *Pinus strobus*, *Quercus coccinea*, and *Betula papyrifera*.

Bog-sedge society.—Toward the center of the bog is a considerable area in which the water level lies just at the surface. The sphagnum is for the most part submerged, and the dominant plants are *Carex oligosperma* and *Scheuchzeria palustris*. Occasional plants of the following society are scattered throughout.

Bog-shrub society.—While this zone is characterized by *Chamaedaphne calyculata*, *Sphagnum cymbifolium*, *S. recurvum*, and *S. subsecundum*, young and dwarfed specimens of the spruce, tamarack, and pine are present in large numbers. The surface formed by the sphagnum is exceedingly rough and marked by hummocks. Among the depressions *Eriophorum virginicum*, *E. vaginatum*, *Andromeda polifolia*, *Sarracenia purpurea*, and *Oxycoccus macrocarpus* are abundant.

Tamarack-spruce society.—This society forms a zone completely surrounding the shrub society, and is dominated by trees of *Larix laricina* and *Picea Mariana*. Occasional specimens of *Pinus Strobus* are found, especially toward the southwest corner, where the substratum is somewhat higher than elsewhere. Beneath the trees is an almost impenetrable tangle of shrubs, especially *Vaccinium corymbosum* and *Ilicioides mucronata*. The substratum is practically bare of lower vegetation. An occasional mat of *Aulacomnium palustre* may be found at the tree bases. That this society will come into possession of the central bog area is certainly indicated by the great numbers of young trees among the bog shrubs.

Willow-sedge society.—As usual in the clearing of the adjacent land, the larger trees of the bog margin were also removed, and in their stead has come up a growth of willows. The dominant plants of this zone are *Salix sericea*, *Cornus stolonifera*, *Spiraea salicifolia*, *Salix discolor*, *Carex riparia*, and *C. stipata*. Associated with these plants are *Sambucus pubens*, *Salix nigra*, *Iris versicolor*, *Populus monilifera*, *Dryopteris spinulosa intermedia*, *Osmunda cinnamomea*,

Equisetum limosum, *Cornus candidissima*, *Aronia nigra*, *Rosa Carolina*, *Juncus effusus*, *Calamagrostis canadensis*, *Rubus strigosus*, *Illicioides mucronata*, *Comarum palustre*, *Carex filiformis*, *Panicularia canadensis*, and *Poa flava*. Forming a high border about the tamaracks and spruces are numerous large plants of *Vaccinium corymbosum* and *Illicioides mucronata*.

The very marked difference between the vegetation of the central and marginal parts of the bog are worthy of especial note. The former represents the original vegetation of the bog. The latter illustrates most forcibly that under present conditions a very different set of plants springs up and becomes dominant, in spite of the fact that the true bog plants were near at hand when the clearing occurred. This bog also illustrates that stage in the filling of a depression immediately following the disappearance of the lake.

In other bogs near Oxford, *Dasyphora fruticosa* and *Chiogenes hispidula* occur among the shrubby growth.

THE DELHI MUSKEAGS.

In the bog north of Delhi which has already been described occur two areas, somewhat to the west of the lakes, which seem to represent a later stage in the history of a bog than that shown by the lakes. These areas, if they were found in northern Michigan, would be termed "muskeags." They are surrounded by large tamaracks, and small tamaracks occur throughout, the smallest specimens toward the center. If the bog at Oxford were to continue its work of filling until the central society disappeared, we should have a bog area of much the same appearance. The small tamaracks stand far apart, and between them is a most luxuriant growth of *cassandra* and sphagnum. The hummocks rise between 3 and 4 feet (0.9–1.2^m) above the substratum. As one attempts to traverse these areas, he sinks knee-deep in the long, fibrous, peat moss.

The total number of species is very small, and includes, besides those already mentioned, *Andromeda polifolia*, *Sarracenia purpurea*, *Oxycoccus macrocarpus*, and a few specimens of *Vaccinium corymbosum*.

BOG ON CARPENTER ROAD

This bog is situated in the SW. $\frac{1}{4}$ Sec. 36, Ann Arbor Tp. Its basin is a small depression in the glacial moraine occupying about

one-tenth of an acre (fig. 10). On the south, west, and north sides it is bordered by clay hills which rise 25 to 40 feet (7.5–12^m) above the bog level. The vegetation of the hills is dominated by *Quercus velutina*, *Q. alba*, and *Q. rubra*. With these trees occur *Hicoria ovata*, *Hamamelis virginiana*, etc.

On the north side the upland has been cleared, and the land is

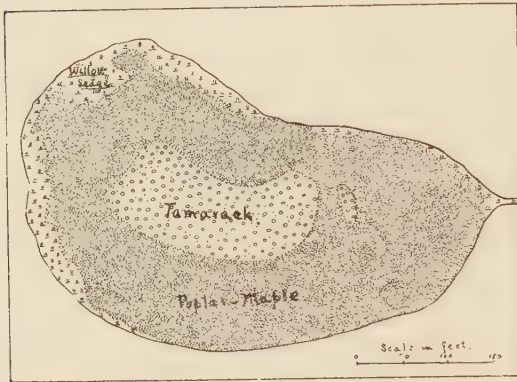


FIG. 10.—Bog on Carpenter road.

now under cultivation. From time to time tamaracks have been removed from the bog, until at the present time only the central area remains to indicate the original covering. Accompanying the clearing there has grown up about the tamaracks the usual thicket of shrubs and young

trees. As elsewhere, the peat is more thoroughly decayed and the substratum level somewhat lower about the margin than toward the center. This fact is of importance in differentiating the willow-sedge society.

Tamarack society.—This society is dominated by the group of rather mature tamaracks. The substratum has the characteristic hummocky surface, marked by large exposed roots, common to such areas. It is overlaid by a loose covering of vegetable matter, made up principally of tamarack needles. The undergrowth is sparse, but most of the bog shrubs and herbs are represented. The more important species are *Chamaedaphne calyculata*, *Sphagnum cymbifolium*, *S. recurvum*, *S. subsecundum*, *Eriophorum virginianum*, and *Lycopus virginicus*. A very noticeable growth about the bases of most of the shrubs is produced by the fungus, *Thelephora intybacea*. The mycelium in developing its sporophores rises about the stems, frequently to a height of a foot (25^{cm}). From the cylinder thus formed, irregular fan-shaped pilei are developed, which gives

the appearance of an elongated brown rosette about the stem^s bases. *Clitocybe laccata* and *Boletinus porosus* are also abundant in the autumn. The partially decayed stumps bear *Peltigera canina*. Other species occur in this area, but reach their dominance in the next society.

Poplar-maple society.—Here are brought together the remnant of the bog species, and those more characteristic of swamps and clearings. The trees are mainly *Populus tremuloides*, with a scattering of *Acer rubrum*. Elm seedlings occur. The shrubby plants, however, make up the bulk of the vegetation. *Ilicioides mucronata*, *Ilex verticillata*, *Aronia nigra*, and *Vaccinium corymbosum* have almost complete possession, and are struggling with one another for space. All these forms send up stems from the underground parts, so that among them the struggle is largely a mechanical one. However, where the red maple overtops them, the factor of shade enters, and the black choke-cherry and high-bush blueberry are the most tolerant. The mountain holly and black alder prevail elsewhere. The next most important plants are the willows, *Salix sericea* and *S. discolor*. Mixed with these are *Cornus candidissima*, *Rubus nigrobaccus*, *Rosa Carolina*, *Cornus stolonifera*, *Spiraea salicifolia*, and *Rubus strigosus*.

Willow-sedge society.—The area dominated by these plants is covered with water in the spring and during moist weather. Although this society is fast being crowded out by the next preceding, it is probable that only a small part of that area was ever occupied by these plants. These plants require a more moist substratum. The dominant species are *Salix sericea*, *Carex riparia*, *C. stipata*, *Cornus stolonifera*, and *Osmunda cinnamomea*. In the case of the cinnamon fern found in this bog there is a remarkable development of aerial roots. They are about an inch long and extend outward from the thick rootstock in all directions, forming a dense covering. The roots are thickly covered with root-hairs which have been persistent at least through one winter. The root-hairs are large and brown in color. The appearance of these rootstocks, as a whole, is very suggestive of certain tropical tree ferns. The other species present are *Ranunculus abortivus*, *Polygonum sagittatum*, *Cicuta bulbifera*, *Prunella vulgaris*, *Rubus americanus*, *Rhus Vernix*, *Solanum dulca-*

mara, *Impatiens biflora*, *Eupatorium perfoliatum*, *Calamagrostis canadensis*, *Dryopteris thelypteris*, *D. spinulosa intermedia*, *Doelingeria umbellata*, *Lactuca spicata*, *Coptis trifolia*, *Boehmeria cylindrica*, *Onoclea sensibilis*, *Marchantia polymorpha*, and *Rosa Carolina*.

The further development of these societies under present conditions will bring about a complete change. There can be no doubt that the poplars and red maples are the coming trees, with elm a close third. When these have become sufficiently large and numerous to overshadow the shrubs, the latter will be killed out, and we shall have in their place the maple-elm forest common to the low grounds. The shrubs, however, are capable of persisting for a great length of time, because of the difficulty of tree seedlings obtaining a start beneath them.

THE CHELSEA BOG.

Of the bogs which have been subjected to clearing, burning, and ditching, by far the most interesting in this region is located just to the southeast of the town of Chelsea. It covers an area of about 50 acres (20 hectares), and the peat is reported to be 40 feet (12^m) thick at the deepest places. The divisions into societies, as indicated on the map (*fig. 11*), are based on the most general characters of the vegetation. There are gradations between all of the societies, and these are so gradual that it is difficult to determine definitely the boundaries. Further, owing to the tendency of many of the shrub species to form dense local growths by the development of stems from underground shoots, the smaller associations are very diverse in different parts of the same society.

Birch-vaccinium society.—This mixed society of bog shrubs occupies about one-fourth the area of the bog. Its substratum consists of peat standing about a foot above the average water level. The dominant plants are *Betula pumila*, *Vaccinium corymbosum*, *Rubus frondosus*, *Aronia nigra*, *Vaccinium canadense*, and *Pteridium aquilinum*. Just as common perhaps, but of lower growth, are *Rubus hispidus*, *Spiraea salicifolia*, *S. tomentosa*, *Aralia hispida*, *Chamaedaphne calyculata*, and *Rumex Acetosella*. The ground covering, except beneath the dense shade of the shrubs, is made up of *Polytrichum juniperinum*. There are many small areas of which this plant now holds exclusive control, and forms a rich carpet of

green, yellow, and red, depending upon the season of the year. Where the moss is disturbed by the uprooting of plants, the substratum becomes exceedingly dry. The moss dies out, and in place of it there springs up a growth of *Cladonia rangiferina*, *C. pyxidata*,



FIG. 11.—Chelsea bog.

C. gracilis, *C. verticillata*, *C. cristatella*, and frequently a small admixture of *Rumex Acetosella*. These plants gradually close over the surface and aid in the conservation of the moisture. As the conditions become more favorable, the *Polytrichum* again closes over the area, driving out the lichens. About the borders of the shrubs

the *Polytrichum* is killed out by the shade. *Rumex Acetosella* is better fitted to withstand such conditions, and consequently forms an inner border about each group of shrubs. Where depressions occur and are flooded for any length of time, the *Polytrichum* is replaced by *Eriophorum virginicum* and *Scirpus cyperinus*. Along the northwestern border *Rubus nigrobaccus* is making inroads upon this society. To the north of the railroad, however, the most important changes are being wrought by the development of *Populus tremuloides* and *Quercus velutina*. Young trees of the former are now scattered throughout, while the latter is present in small number. The plants of minor importance are *Ilex verticillata*, *Viburnum lentago*, *Ilicioides mucronata*, *Amelanchier Botryapium*, *Euthamia graminifolia*, *Doellingeria umbellata*, *Bidens trichosperma tenuiloba*, *Dulichium arundinaceum*, *Poa flava*, and *Sphagnum cymbifolium*.

Chokeberry society.—*Aronia nigra* forms the most dense and exclusive growth that occurs on the bog. Usually the substratum is somewhat lower and more subject to overflow than in the last society. It would seem from observation that this condition is in part due to the chokeberry itself. Owing to its dense growth, it protects the surface of the peat from drought and favors the processes of decay. At the same time it adds very little to the substratum in the way of débris. Where it attains its best development it is practically without undergrowth. About the borders it is mixed with *Vaccinium corymbosum*, *Betula pumila*, and *Ilex verticillata*. Of the smaller plants, *Pteridium aquilinum* penetrates to the greatest distance. Other species occurring about the borders are mentioned among the other societies.

Poplar-willow society.—About the borders of the bog, and extending to a greater or less extent into its interior, is a dense zone composed of *Populus tremuloides*, *Salix discolor*, *Quercus velutina*, *Populus grandidentata*, and *Salix nigra*. By far the most abundant form is the trembling aspen. The substratum varies from areas well above the water level to areas which are constantly submerged. The aspen is also the most important of the plants which are invading the shrub societies. In the relative proportion of the individual species there is the greatest variation at different places in this border zone. Of the more enduring species, *Quercus velutina* is the most abundant. The other species present are *Salix Bebbiana*, *S. sericea*, *S. lucida*,

Prunus serotina, *Quercus alba*, *Q. macrocarpa*, *Acer rubrum*, *Betula lutea*, *Amelanchier*, *Botryopium*, *Viburnum pubescens*, *Spiraea salicifolia*, *S. tomentosa*, *Corylus americana*, *Sambucus pubens*, *Cornus candidissima*, *C. stolonifera*, *Cicuta maculata*, *Aster lateriflorus*, *Carduus altissimus*, *Galium asprellum*, *Osmunda cinnamomea*, *O. regalis*, *Ranunculus pennsylvanicus*, *Calamagrostis canadensis*, *Viola blanda*, *Euthamia graminifolia*, *Bidens frondosa*, and *Aster Novae-Angliae*.

Sedge society.—On the northeast side of the bog is an area dominated by sedges. In the fall of the year it appears to be a uniform area of *Scirpus cyperinus*, but there are many other species mixed with it. The substratum is low and is mainly characterized by tussocks formed by the sedges. Throughout, occur small clumps of the willows already mentioned. The most abundant accessory species are *Isnardia palustris*, *Calamagrostis canadensis*, *Carex teretiuscula*, *C. stipata*, *C. filiformis*, *C. fusca*, *C. oligosperma*, *C. riparia*, and *Aulacomnium palustris*.

The future flora of this bog appears to be indicated by the rapid growth of the poplars, willows, and oaks. The few tamaracks remaining are approaching maturity and are not being reproduced. The means by which these tree species combat the shrubs is mainly by shading, while the latter in the same way interfere with the development of the tree-seedlings. The time involved in this struggle must be very great, but the ultimate outcome will be an oak forest, the intervening stages being filled in by poplar and willow growths. If, however, the decay of the peat beneath these trees brings the surface to the water level, the poplar-willow stage will be indefinitely prolonged.

GENERAL CONSIDERATION OF THE BOG FLORA.

Beside the trees mentioned in the preceding descriptions, note should be made of the occasional occurrence of the black ash, *Fraxinus nigra*, and swamp white oak, *Quercus platanoides*, in bog areas. It frequently happens, when the tamaracks are cut, that the black ash becomes abundant, as in the area one-half mile southeast of Kavanaugh Lake, where it is now associated with *Ulmus americana* and *Acer rubrum*. Another example occurs about a mile north of Chelsea in the NE. $\frac{1}{4}$ Sec. 1, Sylvan Tp. Here in a small area from which the tamaracks were removed, *Fraxinus nigra*, *Quercus platanoides*,

Fraxinus americana, *F. pennsylvanica*, *Acer rubrum*, *Ostrya virginiana*, *Tilia americana*, and *Liriodendron tulipifera* are associated. The undergrowth consists of *Solidago patula*, *S. neglecta*, *Aster lateriflorus*, *Mitella diphylla*, *Euonymus obovatus*, *Viola pubescens*, *Agrimonia hirsuta*, *Cornus florida*, *C. candidissima*, *Eupatorium perfoliatum*, *Rosa Carolina*, *Viburnum Lentago*, *Juniperus communis*, and *Spiraea salicifolia*. The substratum is almost entirely occupied by mosses, including *Hypnum fluitans*, *H. Schreberi*, *H. Blandovii*, *H. roseum*, *Thuidium recognitum*, and *Climacium americanum*.

On the farm of James Barton (SW. $\frac{1}{4}$ Sec. 2, Lyndon Tp.) the black ash, red maple, and American elm have replaced a former growth of tamaracks and black ash.

In a previous publication (55: p. 403) the writer called attention to the absence of a genetic relationship between the bog plants and the surrounding vegetation in southern Michigan. This was explained on the basis that the bog vegetation is a relict of former climatic conditions; that it has a genetic relationship with the conifer forest formation of northeastern North America, as shown by studies in northern Michigan and Pennsylvania, and that in this region it has been surrounded by a more southern flora whose center of distribution is the southeastern United States. Consequently no order of succession between the tamarack and the oak floras is to be expected.

When, however, bog areas are cleared or their normal development disturbed, such trees as the black ash, white ash, red maple, and elm replace the tamarack, and a definite order of succession is established.

It was also maintained that present bog habitats are continuations of similar habitats which came into existence when a colder climate prevailed than at present. More recent observations tend to confirm and strengthen this statement.

The dominance of bog and swamp plants respectively in adjoining areas is to be explained largely by the time when the areas came to support their present ground vegetation. If the habitat has existed undisturbed since the time when a colder climate prevailed, the bog plants will be dominant. If it came into existence in recent times, or has been disturbed, it will be dominated by swamp species.

(To be concluded.)

THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY.

EDGAR NELSON TRANSEAU.

(WITH SIXTEEN FIGURES)

[*Concluded from p. 448.*]

IV. The ecological characteristics of the bog flora and their causes.

The plants occurring in the bog habitat are almost all perennials. In the case of the herbaceous vegetation, the winter is passed by means of subterranean rootstocks. The shrubs are in part evergreen and in part deciduous. The tamaracks and the two birches are deciduous, and the black spruce and pine are evergreen.

Most of the herbaceous and shrubby forms multiply abundantly by vegetative shoots of one form or another. The length of the underground stems of the shrubs is proverbial, but is best appreciated by one who has attempted to dig up one of them entire. In connection with the competition between species for space in the habitat, this is of the greatest importance. A luxuriant growth of cassandra furnishes the most favorable situation for the development of sphagnum in this vicinity. Its profuse branching affords a framework for the upbuilding of the sphagnous layer, its shade properties do not interfere with the photosynthetic work of the moss, and it protects it from the drying effects of wind and direct insolation. Where such associations occur, the difficulties presented for the germination for most seeds, and the efficiency with which competition is combated, are evidenced by the fact that, among the tree species only the tamarack, spruce, and pine are successful invaders. All of these plants send out adventitious roots from the stems and branches, and so keep pace with the upward development of the moss. The absence of poplars, willows, red maples, and elms in such *undisturbed* situations must be in part attributed to the completeness with which such territory is controlled by the cassandra-sphagnum association.

ECOLOGICAL ANATOMY.

Aside from the purely aquatic forms which have received much

ecological attention, it is of interest to look at the anatomical characteristics of certain of these plants.

Eriophorum virginicum may be taken as a type of this group, and also of the sedge zone vegetation in general. The culm is very slender and erect, leaves flat, and very narrow, perennial by root stocks. *Stem*: epidermis very thick-walled and cuticularized. As development proceeds, certain radial rows of the primary cortex cells have their walls thickened, and served to connect the tissues of the central cylinder with those of the three or four outer layers of hypodermal cells which also become thick-walled. Between these radial groups of cells lysigenic air cavities are formed. *Root*: epidermal cells in part thin-walled and in part secondarily thickened, no definite arrangement of the thick-walled cells apparent; internal structures closely resemble those of the stem; no mycorrhiza present. *Leaf*: outer epidermal cell walls strongly thickened and cuticularized, radial and inner walls less so; lysigenic air spaces traverse the leaf longitudinally; a very thick layer of stereome adjoins the leptome, decreasing to one or two cell layers on the hadrome side of the bundle; chloroplasts massed among the outer layers of the cortex, but occur throughout.

Sarracenia purpurea.—Well known for its insect-capturing pitchers. *Stem*: epidermis and first hypodermal layer thick-walled; lysigenic air cavities throughout pith and cortex; resin deposits confined to the epidermis and one or two hypodermal cell layers, but where wounded heavy deposits of resin take place in the exposed and underlying cells. *Root*: cell walls firm, resinous bodies present throughout, but especially prominent in the two outer cortical layers, in which the cell walls are also strongly thickened. *Leaf*: epidermis thick-walled and slightly cuticularized; stomata on both sides of the lamina, with guard cells strongly cuticularized and slightly protuberant; resinous deposits throughout; inner face of lamina with strong downward pointing bristles.

Oxycoccus macrocarpus.—*Stem*: pith thick-walled, with resinous bodies; a thick layer of broad-celled bast forms a complete cylinder within the epidermis. *Leaf*: margins revolute, upper epidermis without stomata, heavily cuticularized, radial walls thick, wavy; hypodermal collenchyma of two or three cell layers on leptome side

of midvein, one or two cell layers on the side of the hadrome, development of the stereome cells also smaller on hadrome side; palisade of two cell layers; lower epidermis covered with wax, especially at the stomata, guard cells slightly elevated. Mycorrhiza present in the larger roots, wanting in the hairlike branches, no root hairs.

Andromeda polifolia.—*Leaf*: margins revolute, upper epidermal cells thick-walled, radial walls undulate, no stomata; lower epidermis supplied with unicellular short stiff hairs, and covered with wax, stomata slightly protuberant, strongly cuticularized beneath midvein; palisade of three layers of long narrow cells; stereome strongly developed above and below vascular bundle; on the ventral side this adjoining three layers of large thin-walled air cells and a one-layered hypoderma. *Root*: resinous deposits throughout, no mycorrhizal fungi found.

Chamaedaphne calyculata.—*Leaf*: margin slightly revolute, epidermis thick-walled, heavily cuticularized, cuticle rough, no stomata on upper surface; ventral epidermis covered by shield-shaped multicellular hairs, and a deposit of wax; cuticle unusually thickened beneath the midvein, guard cells sunken, subsidiary cells protuberant; palisade tissue of four or five layers. *Root*: inner and radial walls thickened, cortical tissues thick-walled; resin deposits in vascular bundle and cortex; no mycorrhizal fungi found.

Chiogenes hispidula.—*Leaf*: margin revolute, epidermal walls very thick, cuticle present, papillate, palisade not strongly developed; mesophyll cells in part thick-walled and in part thin-walled; resinous bodies in the epidermis; stomata slightly protuberant. *Stem*: resin present in cortex; mycorrhizal fungi in the epidermis of the smaller roots and throughout the cortex of the larger.

Vaccinium corymbosum.—*Leaf*: cuticle present, epidermal walls not thickened, palisade of one layer, mesophyll tissues with resinous bodies, cuticle of ventral surface papillate; abundant unicellular hairs on lower epidermis few on upper; leptome side of midvein adjoined by three layers of stereome and two or three layers of hypodermal collenchyma, on the hadrome side reduced to two of stereome and two of collenchyma, cuticular papilli usually developed beneath the midvein and at edge of leaf. *Root*: cortical tissue with resin, mycorrhiza present. No resin deposits found in stem.

Salix sericea.—*Leaf*: upper epidermal cells small, strongly cuticularized; mesophyll compact, palisade of two layers of long narrow cells; stomata on under surface, guard cells sunken beneath the slightly protuberant companion cells; hypoderma of five- or six-cell layers on hadrome side, and eight layers on leptome side of midvein. *Root*: resinous bodies present in medullary rays and cortex, the latter consisting of thick-walled cells; no mycorrhiza.

Ledum groenlandicum.—*Leaf*: upper epidermis rugose, with scattered unicellular hairs, margins strongly revolute, cuticle present, cell walls thickened, the radial walls being broadly undulate; lower epidermis covered with a thick cuticle and a felt of long multicellular and short unicellular hairs, glandular hairs usually present near the small veins, stomata protuberant; palisade of three or four layers of broadly oblong cells; beneath vascular tissue of midvein and between the mestome bundles occur large air cells which may form lysigenic air cavities in the older leaves. *Root*: mycorrhizal.

Larix laricina.—*Leaf*: bifacial, deciduous; epidermis thick-walled, slightly cuticularized, guard cells sunken beneath the companion cells; palisade tissue developed toward the dorsal surface, two layers thick showing a radial tendency, stereome reduced to a few cells beneath the leptome; two resin ducts near edges of leaf. *Root*: composed of mycorrhiza, resinous deposits throughout, cortical tissues early destroyed by fungus. When grown in culture solutions and well aerated, normal roots with root hairs are produced.

Picea Mariana.—Plants in bogs are stunted. *Leaf*: epidermal cells thick-walled, cuticle present, guard cells sunk beneath the companion cells; mesophyll cells compact, of a more or less radial palisade type. *Root*: mycorrhizal, resin deposits throughout, cortical tissues destroyed by fungus. Normal roots are developed under culture conditions.

Pinus Strobus.—Plants very much stunted in the bogs, leaves shorter and thicker. *Leaf*, epidermal walls so greatly thickened that scarcely a lumen remains, beneath this a hypodermal layer of thick-walled cells; mesophyll cells compact and of the usual lobate type. *Root*: mycorrhizal, cortical tissues traversed by the fungus hyphae; resinous deposits throughout. *Stem*: annual rings narrow

dan distorted, resin bodies throughout cortex and meristematic tissues of the wood.

To summarize these characteristics, it is evident (1) that epidermal and hypodermal tissues are thick-walled; (2) that for the conservation of water these are reinforced outwardly by a heavy cuticle, by coverings of wax and air containing hairs; (3) that resinous bodies are found in the roots and leaves of many of the plants; (4) that there is a general reduction in the size of the leaves, and that these are frequently revolute-margined; (5) that palisade tissue is quite uniformly developed; (6) that mycorrhizal fungi are present in the roots of most of the plants; (7) that, when compared with the xerophytes of dry sand plains (25, 6), they show a similarity in respect to the reduction in size of the foliage, in the development of external protective coverings of the sub-aerial parts, and in the presence of palisade tissues, but are very different in the matter of root development and character of root structures.

To account for the peculiarities of the bog vegetation various theories have been brought forward. KIHLMAN (28), in accounting for the xerophilous character of the plants of arctic swamps, which include several species common to American bogs, lays stress upon two factors: (1) the low temperature of the moist substratum, and (2) the presence of drying winds. The former influences the plants by decreasing the power of absorption, the latter increases the rate of transpiration. The plants of such habitats must therefore be protected against the loss of water by the subaerial parts.

SCHIMPER (44, p. 11) in classifying the natural habitats in which xerophytes occur mentions among others "peat bogs, because of the humous acids in the soil." On page 18 he says:

The xerophilous character of the vegetation of peat moors has hitherto been considered an incomprehensible anomaly, and yet the rich supply of humous acids in the soil furnishes a condition for its occurrence as comprehensible as it is necessary. The presence of Scotch pine and heather on both dry sand and on wet peat is thus not more remarkable than is that of *Ledum palustre*, *Vaccinium uliginosum*, and other peat-plants on the cold dry soil in the polar zones.

Further (p. 124) the statement occurs that "on the very acid humus of moors the vegetation assumes a decidedly xerophilous character, because the humous acids impede the absorption of water by the

roots." However, in describing the arctic vegetation (44, pp. 11, 715), he follows the suggestion of KIHLMAN, a conclusion to which he had come independently. GANONG (16) also accepts KIHLMAN's explanation for the xerophilous nature of the raised-bog flora of New Brunswick.

In the study of the structural adaptations of these plants and the causes of their occurrence in bog areas, several questions arise. Are these two factors, cold substratum and acidity, efficient causes of xerophily? Do they act, in the case of the bogs of this region, with sufficient strength to cause xerophilous modifications in the plants there found, or to permit the growth of only such forms as are xerophilous?

The last question may be answered from field observations. They indicate that most low-ground plants grow quite as well on the bog substratum as on the ordinary swamp soils, and that the swamp species of this vicinity may all be found at one place or another growing on bog soils. It would seem that here the bog substratum is no more efficient as a selective agent than are the swamp soils.

The only cases which have come under my observation in southern Michigan which will throw light upon the question of the effectiveness of the temperatures and acidity in the production of xerophilous adaptations is in the case of *Picea Mariana*⁷ and *Pinus Strobus*. These two plants both show reduced size of stem and leaf, in the Oxford bog, when compared with plants growing on the margin. But to what extent this may be due to sterility of the bog substratum rather than to temperature and acidity is indeterminate at this time.

EXPERIMENTS.

To answer the question of the efficiency of a cold substratum and soil acidity to produce xerophily, experiments have been in progress for approximately two years. The difficulties in the way of experimentation along these lines are numerous. The means for controlling soil temperatures in bodies of soil sufficiently large for experimentation with the larger bog plants are practically beyond the possibility of a university laboratory. When it is further realized

⁷ The so-called *P. brevifolia* Pk. This form is certainly no more deserving of a distinctive name than is the bog form of the white pine.

that the experiments should extend over a series of years in the case of the shrubby forms, the problem becomes still more complicated.



FIG. 12.—Average plants from the several cultures of Indian corn. From photographs.

In order to test the relative effects of humous acids (of the concentration found in the bogs of this vicinity) and low substratum temperatures, experiments were made in the form of water cultures

and with a peat substratum. All of the bog water used was brought to the plant house from the First Sister Lake. The acidity of the water varied from .0005 to .0023 normal acid, as measured by $n/100$ KOH solution.

WATER CULTURES.—(1) The plants were grown in four-liter battery jars covered with a plaster of Paris plate, having five one-inch openings for the passage of the plants and one of smaller size for a thermometer. Four such jars were employed in each experiment, two containing a 0.2 per cent. Knop's solution, and the others bog water. One of each was further maintained at a lower temperature. The cooling was accomplished by passing tap water through 15 feet of quarter-inch ($4.5^m \times 7^{mm}$) glass tubing, arranged in a coil within the jar, somewhat below the surface of the liquid. The sides and bottoms of the jars were covered with black paper, and those which were to be cooled were further surrounded by white paper and sphagnum. Daily readings of the temperatures of the air, warm-water solutions and cold-water solutions during the warmest period of the day were recorded. In this way the maximum differences between substrata and air were obtained. As these temperatures were not constant they exaggerate, to a slight degree, the average differences in temperature. Thus, four conditions were obtained which are comparable: (1) warm nutrient solution (temperature approximating that of the air of the plant-house), (2) warm bog solution, (3) cold nutrient solution, and (4) cold bog solution.

Fig. 12 shows the results of one of these experiments with corn. The photograph was taken eighteen days after the experiment was started. When the cultures were set up, the plumule had developed to a length of 2 inches (5^{cm}). The air temperatures during the period of experimentation averaged 18.8° C., that of the warm cultures 18.7° C., and of the cold cultures 10.8° C.

It is to be noted that under these conditions the best growth of the leaves and roots occurred in the bog water. But a reduction of 8° in the substratum temperatures caused a diminution in the development of both leaves and roots; the plants in the nutrient solution and the bog water being equally affected. When all of the plants had developed five leaves, it was noted that in the case of the cold cultures the two lower leaves had withered. This experiment was

repeated with corn, white lupine, and bean under similar conditions, with similar results. The greater development of roots in the case of the warm bog water may be due to the presence of a poison in very minute quantities; but this I have been unable to prove.

(2) A third culture was then made in which five plants of corn were grown in each of the four water culture conditions, and in addition in four similar conditions, using a mixture of sphagnum and peat for the substratum. Wooden boxes 2 feet long, 1 foot wide and a half foot deep ($60 \times 30 \times 15^{\text{cm}}$) were constructed, and two were lined with galvanized iron. The bottoms of the unlined ones were perforated so as to allow of easy drainage. The lined boxes served for the undrained conditions. Further, in one of the drained and in one of the undrained boxes, 40 feet (12^{m}) of glass tubing, bent into coils, the joints being connected by rubber tubing, were arranged so that a constant flow of cold water, for lowering the temperature, could be maintained. The water level in the undrained bog substratum was kept just below the surface. The water was obtained from the bog at First Sister Lake, but occasionally all were watered with distilled water. The amount added to each box was practically the same. In order to keep the solutions in the water culture jars at the same acidity as in the undrained boxes, the water was siphoned off and transferred once a week. Care was taken in this transfer to aerate the water in the boxes as little as possible, while that of the jars was aerated at irregular intervals by means of a bulb. There were thus produced eight conditions, in which it was possible to test the effect of the acidity of the bog water, of aeration (drainage) of the substratum, and of low temperatures. As a result, it was found that the growth of roots and leaves was best in the warm bog water, in the warm nutrient solution, and in the drained warm peat substratum. Reduction in size of both roots and leaves occurred in the cold bog and nutrient solutions, and in the drained cold and undrained warm and cold peat substrata. But the plants in the undrained cold peat showed the most marked reduction in size. The conclusion was reached (1) that humous acids (acidity varying from .0005 to .0023 normal acid) have no effect upon corn in the matter of leaf and root development; (2) that low temperature and lack of aeration of the substratum both cause reduction in size;

and (3) that when low temperature is combined with poor aeration the effect is very marked.

This experiment was repeated with peas, and the same result was obtained, although the effects were not so marked (fig. 13). The roots in the undrained substrata were killed when they attained a depth of a half inch (12^{mm}) below the surface.

(3) In order to test the effects of drainage and of low temperature on bog species, another set of cultures in peat-sphagnum substrata was made. The apparatus used consisted of two flower-pots and two glass dishes approximately a foot in diameter and three inches



FIG. 13.—Effect of the several conditions upon the development of pea seedlings. All are average specimens. From photographs.

deep ($30 \times 7.5^{\text{cm}}$). A flower-pot and a glass dish were kept cool by passing cold water through fifteen feet of glass tubing arranged in coils, as in previous experiments. Three species were tested in these conditions: two-year-old *Larix laricina*, *Rumex acetosella*, and *Prunella vulgaris*. The first cultures were made in the spring of 1903 with the *Rumex* and *Prunella*. The air temperature averaged about eighteen degrees. The cold substratum was maintained about ten degrees lower. In the case of *Rumex* it was found that the largest leaves were produced in the drained peat-sphagnum substratum. Lack of drainage and low temperature both caused a reduction in leaf area, and when combined produced leaves which were less than half as large as those of the drained warm substratum.

The *Prunella* under the same conditions showed the same results.

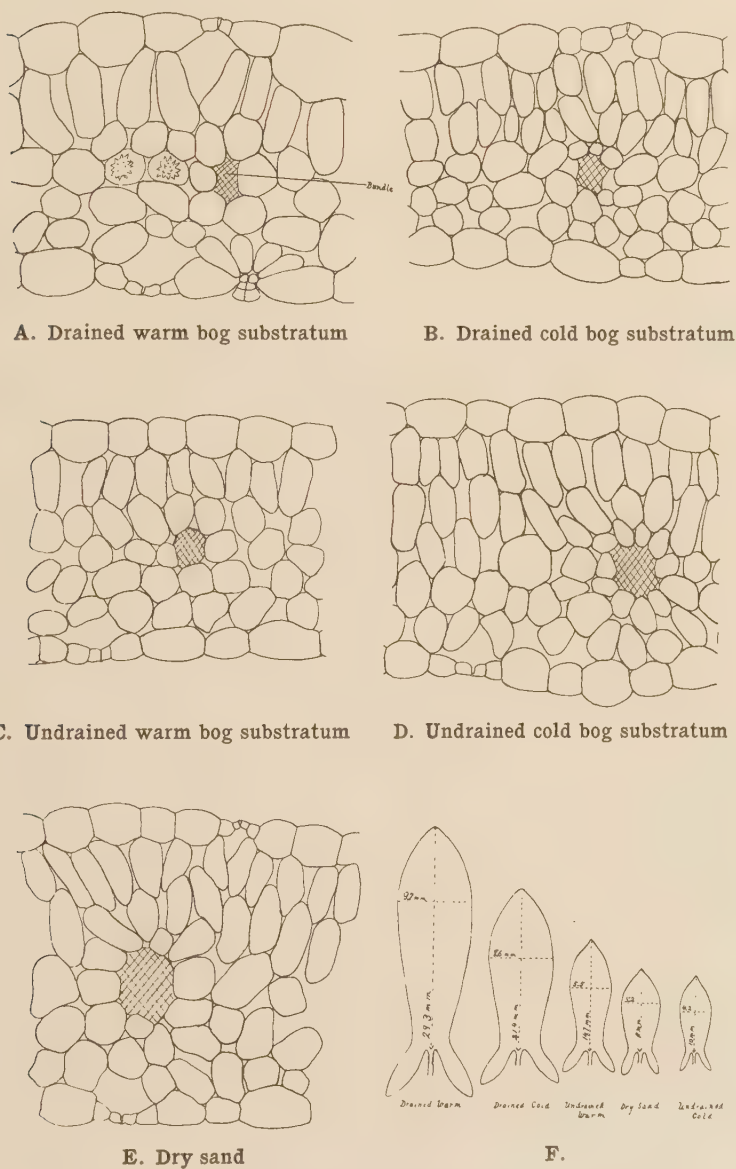


FIG. 14.—A, B, C, D, E, camera drawings of leaf sections resulting from cultures in the five conditions named. $\times 135$. F, diagrams showing average length and breadth of leaves.

Fifteen plants were grown in each condition. At the end of the experiment each had produced six to eight mature leaves. The leaves were measured as to length and breadth. An index was obtained by multiplying these two numbers together and averaging for each culture. Following are the indexes of leaf area thus derived: drained warm substratum 1268.3, drained cold 682.6, undrained warm 518.5, undrained cold 421.8.

In the spring of 1904 the experiment with *Rumex* was repeated. The results correspond with those of the preceding year. The structure of the leaves, resulting in the several cultures, was investigated, and found to show marked variations (56). *Fig. 14* represents the cross-sections and average leaf areas produced (seventy-five leaves being measured in each case). When grown on a warm drained substratum, the leaves are large, and the cells are exceedingly loose and turgid. The epidermis is composed of large thin-walled cells, having a thin cuticle outside. The mesophyll consists of a single layer of palisade and three layers of spongy tissue. No resin bodies are present. The plants grown in the undrained substratum, whose temperature was reduced about 8° C. below that of the air, show marked xerophilous characters. The leaf is reduced in area, increased in relative thickness, and the margins become revolute; the epidermal cells are smaller and outwardly thick-walled; a well-marked cuticle is present; the mesophyll is very compact and made up of two or three layers of well-developed palisade cells and three layers of spongy tissue; and in the epidermal cells and those adjacent to the bundles there are marked accumulations of resinous bodies.

For the purpose of comparison, a corresponding set of plants were grown on sand kept just sufficiently moist to allow the plants to live. As will be seen in *fig. 14*, the xerophily is not more marked than that of the undrained cold bog substratum. *Fig. 15* shows the relative appearance of the plants produced by the different conditions.

In the case of the plants grown in the undrained warm and the drained cold substrata, these same effects were noticeable, but to a less marked degree. That, in the case of the undrained cultures, these effects are not due to the acidity of the bog water is shown by

the fact that plants grown in bog-water cultures develop normally.

The light conditions in the several cultures were the same, direct sunlight being avoided by a cloth screen. It is evident that in this case there is no response to strong light in the development of the palisade tissue (49). It would seem rather to be a response called forth by a reduced transpiration current (44, p. 7). As to function, it may aid in the transfer of food materials as suggested by HABERLANDT (20, p. 260).



FIG. 15.—Average plants showing effect of surrounding conditions. From photographs.

This plant proved to be the most plastic of all of the species used in the experimentation, and was the only one which showed marked variation in the internal structures. Ecologically the results indicate (1) that an undrained peat substratum may cause xerophilous structures, but that the effect is to be correlated with lack of aeration of the substratum rather than with the acidity; (2) that the same effect may be induced by lowering the substratum temperature (the air temperature remaining the same), and thus impeding the rate of

root growth and absorption; (3) that a cold undrained bog substratum is analogous to a dry warm soil in that both produce physiological drought; (4) that resin bodies, which are characteristic of the bog plants, may be produced by this environment in a plant which under favorable conditions is without them.

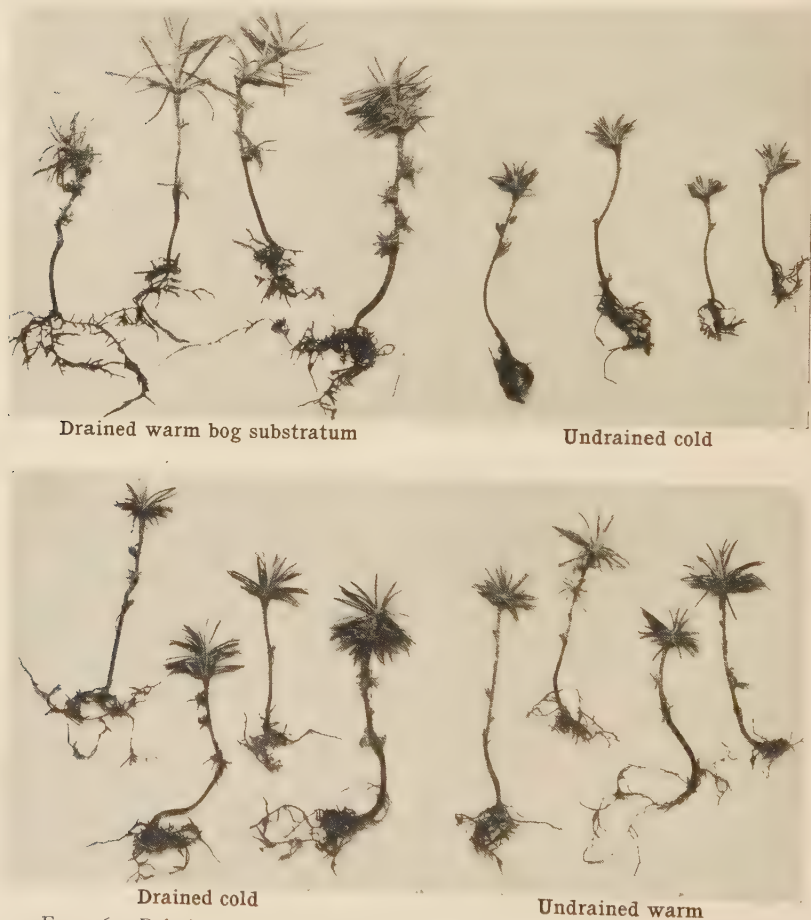


FIG. 16.—Relative effects of drainage and reduced substratum temperature, on *Larix*. From photographs.

The seedling tamaracks, ten of which were cultivated in each of the four conditions just described for the *Rumex*, also showed considerable variation. Their relative development at the end of forty-

four days is shown in fig. 16. The leaves of the drained warm substratum have an average length of 12.6 mm, of the drained cold 10 mm, of the undrained warm 11.4 mm, and of the undrained cold 6.3 mm. Internally, the leaves show a reduction in the intercellular spaces and in the size of the cells in the case of the plants grown on the undrained cold substratum, when compared with those of the warm drained condition.

(4) In another series of experiments with plants of *Larix* four to five years old practically the same results were obtained. There were the greatest number and length of leaves and branches produced in the case of the drained warm substratum. The smallest and shortest leaves and branches were produced by the undrained cold substratum.

Experiments with *Ledum Groenlandicum*, *Chamaedaphne calyculata*, *Andromeda Polifolia*, *Betula pumila*, and *Oxycoccus macrocarpus* have failed to produce satisfactory results. This is believed to be due to the shortness of the time under which they were under cultivation. The plants were brought from the bogs in the late autumn and placed in cold frames over the winter. About the beginning of March they were brought into the greenhouse, and after a few days planted in the warm and cold, drained and undrained boxes, previously described. They have grown vigorously, but the differences noticeable may not be correlated with the four conditions. The cranberry has shown the greatest amount of plasticity, but this could not in all cases be correlated with the environment. If these plants can be kept under known conditions for two or more years, it is probable that they will yield valuable results.

(5) In order to test the effect of mineral soils, and the ability to withstand the presence of large quantities of calcium and magnesium, specimens of andromeda, cassandra, and cranberry were grown in sandy loam and sand. They were watered daily with tap water. The cultures were started in the autumn of 1902, and produced vigorous vegetative shoots during the summer of 1903. They failed to bloom, however, and although they are growing well at this time (June 1904), they have again failed to bloom. This may be in part due to the warm plant-house conditions. The experiment was originally started to observe the changes in the roots, and in so far

have been of value. In a sphagnum substratum all three of the plants produced hairlike roots which attain a length of 5-7^{cm}. The roots are commonly several times branched, very little difference in thickness being shown by the several branches. When grown in sand the roots are still slender, but the frequency of branching is enormously increased. Usually the branching occurs just back of the growing tip. The older root ceases growth as the lateral root develops. The branch continues for 2-3^{mm}, and it also stops growth with the formation of a second lateral root. The result of this process is a zigzag root showing root branches which have been successively the main root tip. Occasionally several lateral roots develop and the main axis is divided.

(6) The statement that waters containing lime and other mineral salts are unfavorable to the growth of sphagnum has gained wide circulation in ecological literature. Because of the great abundance of lime and magnesia in the waters of this vicinity, I was led to test this fact by growing the sphagnum in tap water and solutions of CaCO_3 . In one experiment the water in a battery jar was saturated with CO_2 , CaCO_3 was added in excess, and the CO_2 was again allowed to pass through the water for thirty minutes. In this solution sphagnum was placed, and it has been growing vigorously for three months, although watered daily with water containing over 100 parts of CaCO_3 to the million. Some of the sphagnum cultures have been running for ten months, and show no signs of deterioration. Whether the sphagnum of this vicinity has become accustomed to the presence of lime, owing to the nature of the soil waters, or whether sphagnum is generally able to withstand such conditions, remains to be proved. Since the above experiments were performed, I have found an account of somewhat similar experiments by WEBER (58), the results of which are the same. It would seem, therefore, that the presence or absence of sphagnum is not to be correlated with the presence or absence of lime.

(7) Among the plants growing in the bogs of this vicinity the following have been found to possess mycorrhiza: *Larix laricina*, *Pinus Strobus*, *Picea Mariana*, *Betula lutea*, *Betula pumila*, *Oxycoccus macrocarpus*, *O. Oxycoccus*, *Chiogenes hispidula*, *Vaccinium corymbosum*, *Ledum Groenlandicum*, *Populus tremuloides*.

In order to get at the conditions which favor or cause the development of mycorrhiza, cultures of *Larix* were made in loose sphagnum, sand, undrained sphagnum, etc. The roots in the many other cultures previously noted were also carefully watched. It has been found without exception that where the plants were grown under properly aerated soil conditions, normal roots developed in place of the mycorrhiza. That the acidity of the bog water has nothing to do with the production of mycorrhiza is shown by the fact that in water cultures of the same acidity as the solution in the undrained peat, the plants develop normal roots. In the case of roots developed in loose sphagnum, sand, and moist air, an abundance of root hairs were produced. The normal roots in *Larix* have a diameter about three times that of the mycorrhiza, so that when they begin to develop they appear like white pendants from the dark brown mycorrhiza. That mycorrhiza will not develop in a well-aerated substratum was further tested by the following experiment: Two 30^{cm} test tubes were set upright, and 8^{cm} of glass beads were poured into the bottom of each. Into one a glass tube, at whose end were several small openings, was passed to the bottom. The upper part of the tube was connected with a gasometer. Upon this foundation of beads, three plants of *Larix* were planted in a 5^{cm} layer of peat in each tube. The water level in the two tubes was kept just at the surface, bog water being used throughout. Air was then forced from the gasometer to the bottom of the one tube and allowed to pass slowly through the beads and peat. When the experiment was started, all of the plants possessed only mycorrhiza. In the course of a week the aerated plants began to develop normal roots. The experiment was continued for six weeks. The unaerated plants developed only mycorrhiza, while those which were aerated developed normal roots.⁸ The growth of mycorrhiza is exceedingly slow, and the fungus grows with the root. The development of the above ground parts corresponds to the root development. The plants which produce normal roots have longer shoots, and longer, thicker leaves.

It seems evident, in the case of *Larix* at least, that (1) the mycorrhizas develop only in poorly aerated substrata; (2) their growth is

⁸ In the case of a number of the plants of *Larix* grown in the undrained peat in previous experiments, one or two normal roots were developed just at the surface of the substratum.

exceedingly slow, the fungus developing along with the root; (3) the acidity of the substratum is not a factor in their development; (4) in a naturally well-aerated soil or in an artificially aerated substratum normal roots develop; (5) when the roots are not surrounded by water, root hairs develop abundantly. Mycorrhiza therefore appears to be an abnormal root condition. Whether the fungus is of advantage to the root under these poorly aerated conditions cannot as yet be stated.

(8) In order to determine whether the zone of tamaracks follows the shrub zone because of the occasional submergence of the sedge zone, the following test was made: Ten *Larix* seedlings averaging 7^{cm} in height were placed in a crystallizing dish with the roots imbedded in 2^{cm} of sphagnum. Over this a layer of bog water 4^{cm} in depth was maintained for six weeks. The plants grew quite as well as those in a peat substratum. Stem and root submergence is therefore not a factor in preventing the growth of seedlings tamarack in the sedge zone. The liability to submergence in the bogs I have studied would not extend over nearly so long a period of time.

V. Summary.

The Huron River basin shows three well-marked physiographic divisions which differ in forest covering and the possibilities for bog development. These are (1) the region of the Saginaw-Erie interlobate moraine; (2) the Erie morainic belt; and (3) the lake plain.

In discussing the meteorological conditions of a region as affecting the flora, attention is called to the fact that the significance of the data is not apparent unless the temperature and rainfall phenomena are compared with those of the optimum region of dispersal of the plant societies involved. In the case of the bog plant societies the temperature of the region under discussion averages several degrees higher during the summer months than the eastern maritime provinces of Canada (the optimum region of dispersal for the bog plants), while the rainfall during the same period averages about three-fourths as much. This is believed to account for the general difference in character and development of bog societies in the two regions.

Bog and lake basins are here associated with deposits of glacial drift. The most frequent causes of these basins are (1) the melt-

ing of stagnant bodies of ice in old glacial drainage channels after their abandonment; (2) the differential settling of fluvio-glacial deposits; and (3) unequal deposition of glacial material in moraines and till plains.

Marl and peat deposits are commonly associated. The former are of interest in so far as they aid in the filling of the lake basins. Both are formed through plant agencies.

Peat deposits may be classified under two general heads: (1) those connected with glaciation, and (2) those associated with coastal plain phenomena. In North America the bulk of the deposits come under the first head. Their geographic distribution approximates that of the Pleistocene glaciers. Near the southern border the peat areas are scattered, but they become more nearly continuous and more independent of depressions as we go northward. The same effect is brought about in mountainous regions by increased altitude. In the tundra, peat accumulates because of the low temperature and in spite of the scant vegetation. In temperate regions a vigorous vegetation and areas of stagnant water render peat accumulation possible. In the southern coastal plain swamps, peat is formed in stagnant water because of the luxuriant vegetation and in spite of the high temperature.

During peat formation two processes are involved: (1) *eremacausis* and (2) *putrefaction*. The former is essentially an oxidizing process, brought about in the presence of air by certain fungi and bacteria. Its products are of direct value as food materials for plants. Putrefaction is carried on in the absence of oxygen and is essentially reduction; the organisms involved are anaerobic bacteria, and the products are of no value to the higher plants as food materials. The accumulation of peat depends upon the scarcity of oxygen below the water level, the acidity of the ground water, and the occurrence of low temperatures.

Peat varies in color beneath the various plant societies, being light brown in the youngest (bog sedge) and dark brown in the oldest, the darkest and most thoroughly decayed form being known as "muck." As disintegration proceeds it brings about a decrease in water capacity, a decrease in volatile combustible matter, and an increase in the amount of ash.

The bog as a habitat for plants differs widely from the other plant habitats of the region in that its substratum has been built by fore-runners of the present vegetation. Owing to the influence of the wind in the production of waves, the bogs are largely wanting on the eastern shores of lakes, and in the case of basins which have been almost completely filled with peat, the open water lies toward the eastern margin.

It is well known that bog areas are more liable to late spring frosts than adjoining uplands. This is due to the topography as it affects air drainage, and to the low conductivity of the substratum covering. Under natural conditions it has been found that the areas of *cassandra* and tamarack dominance are more exposed to late frosts than other societies.

Observations in bog areas show that the soil temperatures beneath the several plant societies differ markedly in range. The records indicate that the areas of bog sedges have temperatures corresponding closely with those of the upland and approximating those of the atmosphere. The willow-sedge (swamp) and maple-poplar areas have slightly lower temperatures during early spring. When the trees leaf out, however, the shade produced causes the maple-poplar area to have the lowest temperatures recorded. The bog shrub and tamarack societies show the lowest average temperature throughout the spring months.

Low soil temperatures retard chemical action, diffusion, solution, and osmosis, and render the substratum unsuited to soil bacteria. When coincident with higher air temperatures, plants having a low transpiration ratio are favored in the competition between species.

In so far as southern Michigan is concerned, the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance.

In texture the bog substratum shows every gradation from the coarse fibrous peat of the bog-sedge zone to the black powdery muck of cleared land. Bog soils in general do not afford as good a foothold for trees as do the mineral soils.

Peat is very resistant to the diffusion of mineral salts, hence bog

areas have a very different soil solution from that of the mineral soils adjoining. The high water capacity of peat is detrimental to plants, in so far as it prevents proper aeration of the substratum. Bog waters have no higher osmotic pressure than ordinary soil waters.

The absence of sphagnum from local bogs cannot be explained by the presence of calcium salts, as shown by observation, chemical analyses, and experiments.

The acidity of local bog water varies from .00015 to .00258 normal acid. The lowest values are found in areas covered by bog sedges and swamp plants, and they are approximately the same. The highest occur under the tamaracks. The variations in acidity are related inversely to the temperature. As shown by experiment, this is because of increased oxidation at the higher temperatures. It is suggested that we should find increased acidity as we go north. There is no apparent relation between color and acidity, except that light colored waters usually show slight acidity. The acid nature of the soil solution is a factor in the competition between different species for the occupancy of bog areas.

Bog soils are notably deficient in potassium and available nitrogen. Nitrifying bacteria are prevented from carrying on their normal activities by the acidity of the soil solution, by the lack of oxygen, and by the lower temperature of the substratum.

With few exceptions bog plants are light-demanding forms; hence, in their competition with one another, size and shading ability are prime factors.

That the conditions in the Huron valley are at present not as favorable to the bog plants as to the swamp plants, is shown wherever the two societies come into competition. This fact must be contrasted with the situation in the optimum region of the distribution of bog plants, where the opposite relation has been shown to exist.

An examination of all the physical and chemical data now available fails to account for the differences in flora of bog and swamp areas in this region. The most important factor is believed to be their physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently dis-

turbed, we find the swamp flora, or mixtures of swamp and bog species.

The nature of the bog plant societies of the Huron basin is shown by the description of several local bogs, selected to show both the local bog flora and the variation in societies, and arranged to present the genetic changes in a bog flora as a basin filled by peat accumulation. It is shown that during the early stages of bog development, bog sedge, bog shrub, and conifer societies follow each other in the invasion of the basin. These several societies may vary considerably in composition, but they are closely related and show every gradation in a definite order of succession. The bog conifers, however, show no relationship to the surrounding broad-leaved forests of the upland. On the other hand, where clearing has occurred, swamp sedges, swamp shrubs, and swamp trees gain the ascendancy, and these not only show an order of succession among themselves, but are genetically related to the broad-leaved trees of the region. The bog societies are part of the northeastern conifer forest formation, while the swamp societies are related to the southeastern broad-leaved forests.

An anatomical study of the bog plants shows that epidermal and hypodermal tissues are thick-walled, that a heavy cuticle is present, frequently supplemented by wax and hairs. Resinous bodies are to be found in the roots and leaves of many of the plants. The leaves are usually small and revolute-margined. Palisade tissue makes up a large part of the mesophyll. Mycorrhizas are present in most of the plants. Bog plants resemble the plants of dry sand plains in reduction of foliage area, in development of protective coverings for above-ground parts, and in palisade tissues, but differ from the latter in the matter of root development and root structures.

Experiments indicate that the local bog water itself has no tendency toward the production of xerophilous modifications. Low soil temperatures and lack of soil aeration, however, cause a reduction in the development of the several plant organs. When these two factors are combined, the effect is very marked.

Experiments with *Rumex acetosella* are of especial interest in that nearly all of the characteristics of bog plants may be developed either by lowering the soil temperature, as compared with the air temperature, by preventing proper soil aeration, or by growing in

dry sand. Palisade tissue was developed in the leaves of these plants in diffuse light, and it is shown that palisade tissue is to be correlated with physiological drought. An analogy between the bog habitat and the dry sand habitat is established.

Experiments with *Larix* indicate that mycorrhizas develop only in poorly aerated substrata; their growth is exceedingly slow; the acidity of the substratum is not a factor in their development; a naturally or artificially aerated substratum favors the development of normal roots, and these roots when not surrounded by water develop root hairs abundantly. *Larix* seedlings can withstand prolonged submergence. When exposed to low substratum temperatures and poorly aerated soil conditions, *Larix* produces more xerophilous leaves.

Further field work on the bog plant societies needs to be carried on in the region extending from Winnipeg to New Brunswick. Data on the soil and air temperatures, the acidity, the chemical composition of the soil solution, and the plants associated in bog areas throughout this region will go far toward solving the problems of the distribution of bog plants. Experimentation on the production of xerophilous structures by bog conditions should be continued on a larger scale than is possible in the ordinary university plant-house.

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